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O: 8947

Z: 8979

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TABLE OF CONTENTS

OWEN, R. W. 1989. Microscale and finescale variations of small plankton in coastal and pelagic environments. J. Mar. Res. 47(1):197-240. 8947

OWEN, R. W., N. C. H. LO, J. L. BUTLER, G. H. THEILACKER, A. ALVARIÑO, J. R. HUNTER, AND Y. WATANABE. 1989. Spawning and survival patterns of larval northern anchovy, *Engraulis mordax*, in contrasting environments—A site-intensive study. Fish. Bull., U.S. 87(3):673-688. 8948

PARRISH, F. A. 1989. Identification of habitat of juvenile snappers in Hawaii. Fish. Bull., U.S. 87(4): 1001-1005. 8949

PARRISH, R. H., R. SERRA, AND W. S. GRANT. 1989. The monotypic sardines, *Sardina* and *Sardinops*: their taxonomy, distribution, stock structure and zoogeography. Can. J. Fish. Aquat. Sci. 46(11):2019-2036. 8950

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PEARSON, D. E. 1989. Survey of fishes and water properties of South San Francisco Bay, California, 1973-82. NOAA Tech. Rep. NMFS 78, 21 p. 8952

PERRIN, E. V. D., K. BENIRSCHKE, AND W. F. PERRIN. 1989. Monstrous dolphins—malformations in marine mammals. Teratology 39:51. 8953

PERRIN, W. F. (ed.) 1989. Annex H. Report of the Sub-Committee on Small Cetaceans. Rep. int. Whal. Commn 39:117-129. 8954

PERRIN, W. F. 1989. Newsletter of the Cetacean Specialist Group of the IUCN/SSC. No. 5, 15 p. 8955

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TABLE OF CONTENTS (CONTINUED)

POLOVINA, J. J. 1989. Artificial reefs: nothing more than benthic fish aggregators. Calif. Coop. Oceanic Fish. Invest. Rep. 30:37-38. 8957

—————————. 1989. A debate on responsible artificial reef development. Part III. Should anyone build reefs? Bull. Mar. Sci. 44(2):1056-1057. 8958

—————————. 1989. Density dependence in spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Can. J. Fish. Aquat. Sci. 46(4):660-665. 8959

POLOVINA, J. J., AND I. SAKAI. 1989. Impacts of artificial reefs on fishery production in Shimamaki, Japan. Bull. Mar. Sci. 44(2):997-1003. 8960

RALSTON, S. 1989. Effect of seasonal recruitment on bias of the Beverton-Holt length-based mortality estimator, pp. 190-197. *In* Edwards, E. F., and B. A. Megrey (eds.) Mathematical analysis of fish stock dynamics. Am. Fish. Soc. Symp. 6. 8961

RALSTON, S., AND H. A. WILLIAMS. 1989. Numerical integration of daily growth increments: an efficient means of ageing tropical fishes for stock assessment. Fish. Bull., U.S. 87(1):1-16. 8962

SAKAGAWA, G. T. 1989. Trends in fisheries for swordfish in the Pacific Ocean. *In* Stroud, R. H. (ed.), Planning the future of billfishes. Part 1: Fishery and stock synopses, data needs and management. Mar. Rec. Fish. 13:61-79. Natl. Coalition Mar. Conserv., Savannah, GA. 8963

SCHWING, F. B. 1989. Subtidal response of the Scotian Shelf bottom pressure field to meteorological forcing. Atmosphere-Ocean 27(1):157-180. 8964

SEAMAN, W., JR., R. M. BUCKLEY, AND J. J. POLOVINA. 1989. Advances in knowledge and priorities for research, technology and management related to artificial aquatic habitats. Bull. Mar. Sci. 44(2)527-532. 8965

SEKI, M. P., AND C. S. HARRISON. 1989. Feeding ecology of two subtropical seabird species at French Frigate Shoals, Hawaii. Bull. Mar. Sci. 45(1):52-67. 8966

TABLE OF CONTENTS (CONTINUED)

SKILLMAN, R. A. 1989. Status of Pacific billfish stocks. *In* Stroud, R. H. (ed.), Planning the future of billfishes. Part 1: Fishery and stock synopses, data needs and management. Mar. Rec. Fish. 13: 179-195. Natl. Coalition Mar. Conserv., Savannah, GA. 8967

SKILLMAN, R. A. 1989. Stock identification and billfish management. *In* Stroud, R. H. (ed.), Planning the future of billfishes. Part 1: Fishery and stock synopses, data needs and management. Mar. Rec. Fish. 13: 207-214. Natl. Coalition Mar. Conserv., Savannah, GA. 8968

SMITH, P. E, M. D. OHMAN, AND L. E. EBER. 1989. Analysis of the patterns of distribution of zooplankton aggregations from an acoustic doppler current profiler. Calif. Coop. Oceanic Fish. Invest. Rep. 30:88-103. 8969

SMITH, P. E., H. SANTANDER, AND J. ALHEIT. 1989. Comparison of the mortality rates of Pacific sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, eggs off Peru. Fish. Bull., U.S. 87(3):497-508.. 8970

SOMERTON, D. A., AND D. R. KOBAYASHI. 1989. A method for correcting fish larvae for the size selection of plankton nets. Fish. Bull., U.S. 87(3):447-455. 8971

SQUIRES, D., S. F. HERRICK, JR., AND J. HASTIE. 1989. Integration of Japanese and United States sablefish markets. Fish. Bull., U.S. 87(2):341-351. 8972

STEVENS, E., W. WATSON, AND H. G. MOSER. 1989. Development and distribution of larvae and pelagic juveniles of three kyphosid fishes (*Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea*) off California and Baja California. Fish. Bull., U.S. 87(3):745-768.. 8973

THEILACKER, G. H., AND Y. WATANABE. 1989. Midgut cell height defines nutritional status of laboratory raised larval northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 87(3)457-469. 8974

UEBER, E. 1989. Xanthic, gigantic China rockfish. Calif. Fish and Game 75(1):47-48. 8975

UEYANAGI, S., R. S. SHOMURA, Y. WATANABE, AND J. L. SQUIRE, JR. 1989. Trends in the fisheries for billfishes in the Pacific. *In* Stroud, R. H. (ed.), Planning the future of billfishes. Part 1: Fishery stock and synopses, data needs and management. Mar. Rec. Fish. 13:31-45. Natl. Coalition Mar. Conserv., Savannah, GA. 8976

TABLE OF CONTENTS (CONTINUED)

VLYMEN, L. 1989. Reuben Lasker: a remembrance. Fish. Bull., U.S. 87(3):375-386. 8977

WATANABE, Y., AND N. C. H. LO. 1989. Larval production and mortality of Pacific saury, *Cololabis saira*, in the northwestern Pacific Ocean. Fish. Bull., U.S. 87(3):601-613. 8978

WATSON, W., AND R. L. DAVIS, JR. 1989. Larval fish diets in shallow coastal waters off San Onofre, California. Fish. Bull., U.S. 87(3):569-591. 8979

AU, D. W., AND R. L. PITMAN. 1988. (Omitted in 1988 volume) Seabird relationships with tropical tunas and dolphins, pp. 174-212. *In* Burger, J. (ed.), Seabirds and other marine vertebrates: competition, predation, and other interactions. Columbia University Press, NY. 8880

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BUTLER, J. L., C. A. KIMBRELL, W. C. FLERX, AND R. D. METHOT. 1989. The 1987-88 demersal fish surveys off central California (34°30' N to 36°30' N). U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-133, 44 p.

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TABLE OF CONTENTS (CONTINUED)

EDWARDS, E. F. 1989. Using tuna-vessel observer data to detect trends in abundance of dolphin populations: history and research to date (1988). U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-122, 123 p.

EDWARDS, E. F., AND B. A. MEGREY (eds.). 1989. Mathematical analysis of fish stock dynamics. Am. Fish. Soc. Symp. 6.

HOLT, R. S., AND S. N. SEXTON. 1989. Report of the marine mammal survey of the eastern tropical Pacific aboard the research vessel *David Starr Jordan* July 28-December 6, 1988. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-129, 141 p.

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TABLE OF CONTENTS (CONTINUED)

PERRIN, W. F., R. L. BROWNELL, JR., Z. KAIYA, AND K. JIANKANG (eds.). 1989. Biology and conservation of the river dolphins. Occas. Pap. IUCN Species Surviv. Commn. (SSC) 3, 173 p.

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8947

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Microscale and finescale variations of small plankton in coastal and pelagic environments

by R. W. Owen[1,2]

ABSTRACT

Small-interval water sampling in oceanic subsurface layers in a variety of macroenvironments for microplankton and for characteristics of their environment revealed concentration variations that often exceed errors of sampling and measurement. I report incidence and degree of microscale and finescale organism patchiness and their dependency on the local environment and on certain characteristics of the organisms themselves. Scale analysis indicates that patchiness occurs below as well as above the 20 cm intervals sampled. Incidence and degree of patchiness were about the same in separate eastern boundary regions, off California and Perú.

Effects of environmental characteristics on organism patchiness are clearly defined in this data set, which suggests influences by physical processes on local microplankton patches on the scale of a few centimeters (microscale) to a few meters (finescale). In the aggregate, finescale and microscale patchiness of microplankton populations was greater at lower wind speeds, during daylight than at night, and over continental slopes. Patchiness was greater in the more stable layers of the seasonal pycnocline, and under more oligotrophic conditions (lower concentrations of nutrients, particulates, and chlorophylls). Patchiness of organisms also was greater where nutrients and particulates were more patchy, but was unrelated to chlorophyll patchiness.

Intrinsic properties of the organisms less clearly affected microplankton patchiness. Population patchiness was greater for autotrophs and heterotrophs than for atrophs, and was slightly greater for larval fish competitors and predators than for their prey, and for more motile organisms. Reproductive capacity is indicated to dominate among intrinsic patch-forming attributes.

Smallscale patchiness of small plankton is a recurrent feature of the environment of small predators and may affect their growth and survival. Its incidence and degree appear to be specifiable over large domains from parameters of the mixing environment, e.g. wind stress and vertical stability. This would contribute to management of exploited stocks of marine organisms whose recruitment depends on food supply at early stages of their life-history.

1. Introduction

Starvation rate and growth of survivors in marine animal populations are determined by food supply. Intrinsic rate of natural increase of a population is often thus

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constrained. This supply is defined by encounter rate of predator with prey and by prey composition. Encounter rate is the product of the predator's search rate and the prey concentration. Encounter rate is enhanced where prey patchiness occurs on the scale of the predator's ambit. Prey composition, or "menu," depends on processes that determine the degree to which prey population patches are disjunct or concurrent.

Plankton concentrations are known to vary widely but, with a few exceptions, this knowledge derives from sampling volumes or intervals that greatly exceed those searched by small planktivores, and those over which other ecological processes occur. Models of production, growth, and recruitment that are based on feeding or environment may be futile if the interactions of organisms with one another and with the local environment are estimated from samples drawn at inappropriate intervals of space or time. The presence of small, subsurface patches of microplankton would alter a variety of interactions within and between populations; in particular, predation, competition and reproduction can be differentially affected in the presence of smallscale patchiness. A current hypothesis, for example, holds that small planktivores survive where their food rations appear too low by making use of adequate food patches too small to detect by conventional sampling (e.g. fish larvae: O'Connell and Raymond, 1970; Hunter, 1972; Vlymen, 1977; Lasker and Zweifel, 1978; Houde and Schekter, 1978; copepods: Mullin and Brooks, 1976). The menu, the rations and the consequent survival of predator populations may depend on incidence and degree of patchiness on scales of a few meters (finescale) or less than a meter (microscale).[3] The margins of areas (or volumes) suitable for survival of predators can be considerably extended by the existence of such patchiness. Community characteristics are altered significantly where the living space fluctuates or becomes partitioned by populations so that organisms may co-exist in higher numbers and diversity (e.g. Hutchinson, 1961; Richerson *et al.,* 1970; Roughgarden, 1977). Finescale and microscale plankton patchiness can presumably be created, sustained or destroyed by mechanical processes, biological processes and interactions of the two (cf. Mackas *et al.*, 1985).

This report describes finescale and microscale patchiness of small plankton and of their environment in open waters off southern California and northern Perú on a scale similar to that explored by small fish larvae or copepods over the course of a few hours. I summarize the results of sampling to determine (1) if small predators and grazers encounter microplankton patches during short excursions in the mixed layer and seasonal thermocline of the open sea, and (2) to determine scale and degree of patchiness in the submeter transition between turbulent and molecular domination of diffusion and viscosity. Reported here are parameters of concentration variations detected among microplankton populations and environmental characteristics that were sampled over 2 m transects at 20 cm intervals at 65 sites. I also report sensitivity of the variational parameters of organism concentration to environmental variables and to intrinsic characteristics of the organisms to indicate the mechanisms responsible for their patchiness.

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[3] The descriptive terms "finescale" and "microscale" approximately conform with current usage by oceanographers to describe structure and processes having these respective dimensions (e.g. Haury *et al.*, 1978).

a. Earlier observations. Work on finescale and microscale plankton patchiness has a rather brief history. Microscale plankton patchiness (using Cassie's 1958 definition) was well enough known to occur from direct observation. Published accounts of visual observations include those of Bainbridge (1952), Colebrook (1960), and Clutter (1969) on swarming crustacean populations, and of Owen (1966) on thaliaceans in surface convergences. Less formally, most of us who have paid attention in or near the water have seen plankton aggregations of small extent.

For practical reasons, plankton microstructure was first investigated in lakes. Whitney (1938) found turbid strata of submeter thickness and tens of meters in lateral extent to be common in several Wisconsin lakes. Ruttner and Sauberer (1938), from the correspondence of optical profiles with cell counts, attributed such microstrata in Austrian lakes to variations of phytoplankton and bacteria concentrations. Baker and Brook (1971) later demonstrated correspondence between lacustrine microlayers of turbidity and phytoplankton populations. The existence of small patches of less motile phytoplankton populations in the epilimnion of a California lake was attributed by Richerson *et al.* (1970) to their production rate, indicating that reproduction exceeded dispersion.

With the advent of the o-ring, indirect indications of microscale structure have been made in the open sea by *in situ* profiling of phytoplankton by pigment fluorescence (e.g. Derenbach *et al.*, 1979; Astheimer and Haardt, 1984) and of particulates by light scattering (e.g. Owen, 1972). The volume sensed by instruments deployed in these studies was less than 1 cm^3, so their signal spikes may have been due to individual aggregates or colonies of plankters rather than to patches. Both methods integrate broadly over particle types.

Quantitative works on marine plankton variations based on submeter water sampling were summarized by Cassie (1963) and consist of studies by Cassie (1959, 1962) on horizontal variations of phytoplankton at the sea surface from water capture, and by Della Croce (1959) and Zaitzev (1961) on vertical variations of small zooplankton in the upper meter from net haul samples. Ragotzkie and Pomeroy (1957) found *Gymnodinium* cells confined mainly to the upper 10 cm layer during an estuarine bloom of this dinoflagellate. McAlice (1970) sampled at submeter intervals in the uppermost meter of two estuaries and presented evidence for the existence of coherent phytoplankton patches smaller than a meter. Owen (1981a,b) described variations within 2 m intervals from limited subsets of the data analyzed here. With the exception of these 1981 reports, literature on submeter plankton sampling has been confined to the sea surface (upper meter or less) and to bays, estuaries and lakes. Because plankton communities and physical processes are likely to be rather special in the uppermost meter or in lakes and estuaries, results from these environments cannot reasonably be extended to subsurface, open-sea environments.

b. Regions and design. The Southern California Bight, where much of the sampling was conducted, affords conditions of low wind mixing and thus optimal conditions for maintenance and detection of open-sea microscale structure of plankton populations. The Channel Island groups and Tanner-Cortez Banks, extending southward from Point Conception, constitute a barrier that somewhat shelters the Bight interior from wind and surface wave mixing. A relatively shallow, stable pycnocline is created by insolation and geostrophic uplift, and is maintained by this sheltering effect. By contrast, the Chimbote Shelf off Perú is open to surface and subsurface mixing forces and is broad and shallow, sloping continuously to the shelf break about 100 km offshore. Vertical mixing and upwelling are correspondingly vigorous and physical stratification is weak.

Accordingly, I sampled for subsurface variations in concentration of small plankton and for certain environmental characteristics at 20 cm intervals in a variety of macroscale environments of the open sea. The work was designed to determine the incidence and intensity of microplankton variations in a variety of physical and biotic environments. All of the sampling reported here was conducted in regions of spawning by the sometimes extensive anchovy populations off California (58 casts) and Perú (7 casts). However, neither presence of larval fish nor estimates of larval fish prey were considered in the sampling design. All but four of the 65 casts sampled the vertical axis, over which the greatest degree of patchiness was anticipated. The four horizontal casts were paired with vertical casts to give an estimate of relative variability of patchiness along the two axes.

Sampling was conducted on the coastal shelf, near the shelf-break, and beyond the shelf-break within 200 km of the coast. Depth of the 2 m layer to be sampled was usually predicated within 20 min on results of CTD or chlorophyll profiles to sample the upper seasonal pycnocline, mixed layer, or chlorophyll maximum layer. Shifting of the target layer by internal wave passage may have occurred between CTD and water sampling, but target features usually were broad. Sampling was conducted in all seasons in daylight and at night under light or moderate winds, usually in the absence of waves that would produce surge during sampling (swell <2 m amplitude, <10 s period).

2. Methods

a. Sampling. Samples to assess microscale variations were obtained with a micropatch sampler (MPS) (Owen, 1981) adapted for midwater use from a free vehicle bottom-water sampler design by Sholkovitz (1970). The MPS, shown in Figure 1, consists of a linear array of 4 cm i.d. sampler tubes spaced along a vaned frame fitted

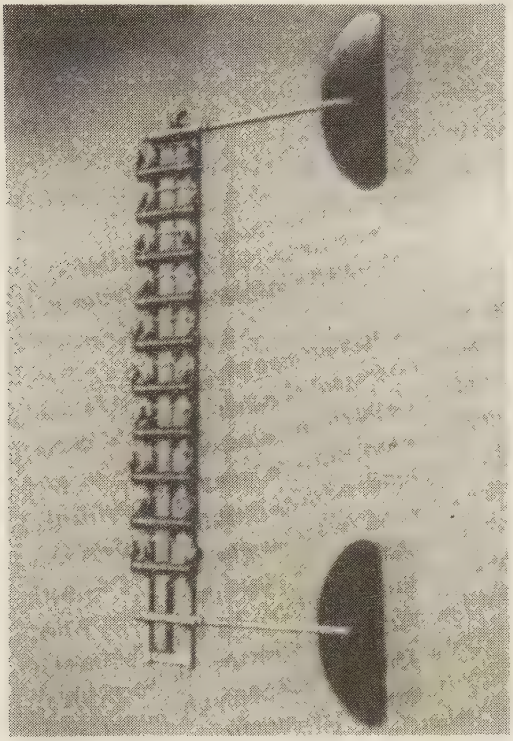

Figure 1. Micropatch sampler (MPS) with sample tubes open. Spring-loaded rod (center of frame) releases ball valve lanyards to close tubes when messenger weight strikes trigger on cable clamp atop MPS frame.

with cable clamps and a lanyard release mechanism. Water samples were retained by ball valves seated at either end of each tube and held by elastic cord connecting the valves through the tube center. Prior to deployment of the MPS, the ball valves were held clear of the tube mouths by lanyards hooked onto pins on the release mechanism.

To sample vertical variations, the MPS was clamped to the ship's hydro-wire ≈10 m above a 45 kg terminal weight, lowered with open sample tubes to the target depth and towed at ≈20 cm/s so that its vanes oriented the tube mouths into the induced current for complete flushing.[4] To sample horizontal variations, the MPS was clamped sideways on the hydro-wire (tubes vertical), lowered below the target depth and retrieved slowly upward through the target depth. A messenger weight sent down the hydro-wire triggered the simultaneous release of lanyards that restrained the ball valves, whereupon the valves seated in the tube mouths and captured 0.6 l of seawater.

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[4] Direct observations of the instrument showed that the sampler remains within 5° of vertical when towed at 20–40 cm/s, and that discrete dye layers are sampled distinctly and are disturbed only in the wake of the instrument.

Upon retrieval of the MPS, water samples obtained from each tube were transferred to covered beakers, mixed thoroughly with a small plunger and then aliquoted for various combinations of analyses. Particular combinations depended on availability of people and equipment, and included plankton enumerations, phytoplankton pigments (chlorophyll-*a* and phaeo-pigments), Coulter particle counts, nutrient salts, and salinity.

To contrast variations along the sampler frame with variations at the same position on the frame, parallel samples were obtained from 40 of the 65 MPS casts by additional tubes strapped alongside the originals at 2–5 positions in the array. Parallel tube centers were 5 cm apart.

The first 37 casts were made with a 10-depth array of sampling tubes spaced at 20 cm intervals[5] between tube centers. The remaining 28 casts were made with an array of sampling tubes spaced at five 20 cm intervals and two 40 cm intervals. (The interval sequence was 20, 40, 20, 20, 20, 20, 40 cm.) This arrangement permitted interspersion of fine-mesh plankton nets among the sampling tubes in the array; the results of their use are to be treated separately.

b. Sample analysis.[6] Plankton preserved in 3% formalin prepared according to Beers and Stewart (1970) was concentrated by sedimentation overnight from known initial sample volumes and enumerated using the inverted microscope method of Utermöhl (1931). Counting was done by either of two methods; the entire slide surface was enumerated, or 20–35 randomly chosen fields were enumerated. Populous organisms usually were enumerated along single transects of the slide. Identical procedures were used when duplicating counts of the same sample to establish error of determination. Original sample volumes were usually 100 ml for enumerating phytoplankton and 400–600 ml for enumerating microzooplankton and rarer phytoplankton species. Organisms selected for counting exceeded 20 μm in longest dimension unless easily seen and identified at 100× using phase contrast on the Zeiss inverted microscope. Identification to species was not always possible, in which case organisms were classified to genus or higher taxon within defined size classes. This report treats only those species that usually occur as individuals except when dividing: colonial forms are ignored. Original microplankton enumerations and corresponding concentration factors are given by Owen and Kimbrell (1987).

Phytoplankton pigments were determined following the method and equations of Holm-Hansen *et al.* (1965). Water samples allocated for pigment analysis were filtered through Whatman GF/C glass fiber filters previously de-sized with distilled water. The filters were placed in vials with 10 ml of 90% aqueous acetone, sealed and extracted in cold and dark for 22–28 h. Fluorescence of phytoplankton pigments was measured before and after acidification of the extracts with dilute HCl. The fluorometer was a Turner 111 with Sylvania F4T5 lamp behind Corning 5-60 excitation filter and red-sensitive Hamamatsu photomultiplier behind Corning 2-64 emission filter.

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[5] It seems more correct as well as convenient to consider MPS data as interval estimates rather than point estimates in view of the dimensions of the spaces sampled.

[6] Reference to trade names in this section does not imply endorsement by the National Marine Fisheries Service, NOAA.

Particle concentrations were determined within an hour after sampling using a Coulter Ta counter with a 280 μm sensing pore to describe their variations in three size categories; 16–160 μm, 32–50 μm, and 51–160 μm equivalent spherical diameter. Total counts usually exceeded 50000 per sample. By overriding the Counter manometer (in the absence of ship's surge) I could analyze sample volumes of 20-100 cc to achieve higher total count levels.

Nutrient salt concentrations were determined by Technicon autoanalyzer or Beckman DU spectrophotometer using procedures of the Physical and Chemical Oceanographic Data Facility (PACODF) of the Scripps Institution of Oceanography (Atlas *et al.*, 1971). Samples either were analyzed within a few hours of collection, or were filtered and frozen for analysis ashore.

Salinity determinations were made ashore after each cruise with the Plessey or Autosal salinometers. Wormley water was used for primary standardization. Duplicate or triplicate determinations were averaged.

Conductivity/temperature/depth (CTD) casts were made at most stations using a Plessey 9040 CTD. To provide good resolution of structure in layers of interest, the CTD usually was fitted with a 300 d-bar pressure sensor and was lowered at 20 m/min. Where CTD casts were not made, Sippican XBT casts (with T-4 probes) were.

All sample analyses and measurements except temperature are expressed in concentration units.

c. *Parameters of variation.* A problem arises in treating the serial data obtained by the MPS because simple parameters of variation do not distinguish between samples drawn from a monotonic gradient and samples drawn from truly clumped distributions. To de-couple gradient effects from patchiness effects, I chose to characterize concentration variations in the following way. I derived the mean concentration gradient and the individual deviations about the gradient by linear regression of sample concentration (dependent variable) on sample depth (independent variable) for each organism population and each environmental characteristic in each MPS cast. The variance removed by the regression is termed finescale variation (*FSV*). *FSV* denotes the regression mean square over the 2 m interval and thus expresses variance accountable to the mean concentration gradient:

$$FSV = \Sigma(\hat{c}_i - \bar{c})^2$$

where $\hat{c}_i$ is the predicted *i*-th sample concentration and $\bar{c}$ is the cast mean concentration. *FSV* connotes meter-scale patchiness.

The residual variance, associated with the deviations of individual concentrations from the mean gradient, is termed microscale variation (*MSV*). *MSV* denotes the mean square of deviations of the observed concentrations about the mean concentration gradient and thus expresses the detrended variance:

$$MSV = \Sigma(c_i - \hat{c}_i)^2/(n - 2)$$

where c_i is the observed sample concentration and n is the number of intervals sampled. MSV connotes decimeter-scale patchiness.

Coefficient of variation (cv) was used to scale the variations between segments of the data set to allow comparisons among variational statistics of concentrations that occur at widely differing levels. The respective cv's are thus the root mean square (rms) values of finescale and microscale variations divided by the cast mean:

$$cv\text{-}FSV = \sqrt{FSV}/\bar{c}$$

and

$$cv\text{-}MSV = \sqrt{MSV}/\bar{c}.$$

Coefficient of variation also stabilizes the variance, otherwise proportional to the mean value in patchy distributions, and is more intuitive and communicable than the variance value.

Coefficients of concentration variation were derived between depth intervals within casts using averaged parallel and duplicate values where these occurred, within the same sample (duplicate determinations) and between samples at the same depth interval from tubes in parallel. Parameters of organism concentration variations were derived from whole-slide and partial-slide counts. This presentation subsequently pools values derived from whole-slide and partial-slide concentrations because AOV showed no difference between them.

Variations due to error of sampling and determination were internally derived: coefficients were constructed for each environmental and population concentration by analysis of variance (AOV) on all parallel sample analyses (error of sampling) and on all duplicate analyses from the same sample bottle (error of determination + subsampling).

The coefficients of variation for parallel samples and duplicate determinations in Table 1 are used to contrast with cv values observed between depths in casts. Mean-square variation between organism concentrations from parallel samples exceeded that between duplicates by average factors of up to 15, depending on the count type and number of organisms counted. This disparity is also evident among the environmental determinations to roughly the same degree. Although the parallel samples were intended to provide an error term for contrast with the between-depth variations, some of the differences between parallel samples reflect real spatial variation due to the 5 cm separation between parallel sample bottles on the MPS frame. The use of mean-square variation between parallel sample determinations as an error term is correspondingly conservative and leads to underestimation of incidence

Table 1. Means ($\bar{c}$), coefficients of variation ($cv = s/\bar{c}$) and mean-square ratios (F) among pairs of parallel sample (parallels) values and duplicate determinations (duplicates) of individual microplankton populations and environmental characteristics. N is number of pairs.

Characteristic	N (pairs)	$\bar{c}$ (no/1)	cv	F
Microplankton				
parallels	371	528	0.665	
duplicates	97	757	0.222	4.4
Chlorophyll-*a*				
parallels	89	2.005	0.131	
duplicates	9	1.657	0.080	3.9
Phaeopigment-*a*				
parallels	89	0.698	0.372	
duplicates	9	0.217	0.400	8.9
Coulter counts (16–160 μm)				
parallels	58	191	0.245	
duplicates	7	532	0.057	2.4
Coulter counts (32–50 μm)				
parallels	58	21.6	0.448	
duplicates	7	95.5	0.120	0.7
Coulter counts (51–161 μm)				
parallels	58	13.1	0.510	
duplicates	7	20.8	0.122	6.9
Nitrate + nitrite				
parallels	26	6.35	0.124	—
Nitrate				
parallels	10	2.50	0.212	—
Nitrite				
parallels	10	0.19	0.107	—
Ammonium				
parallels	17	1.04	0.231	—
Silicate				
parallels	27	702	0.176	—
Phosphate				
parallels	17	157	0.283	—
Salinity				
parallels	15	33.47	0.00053	—

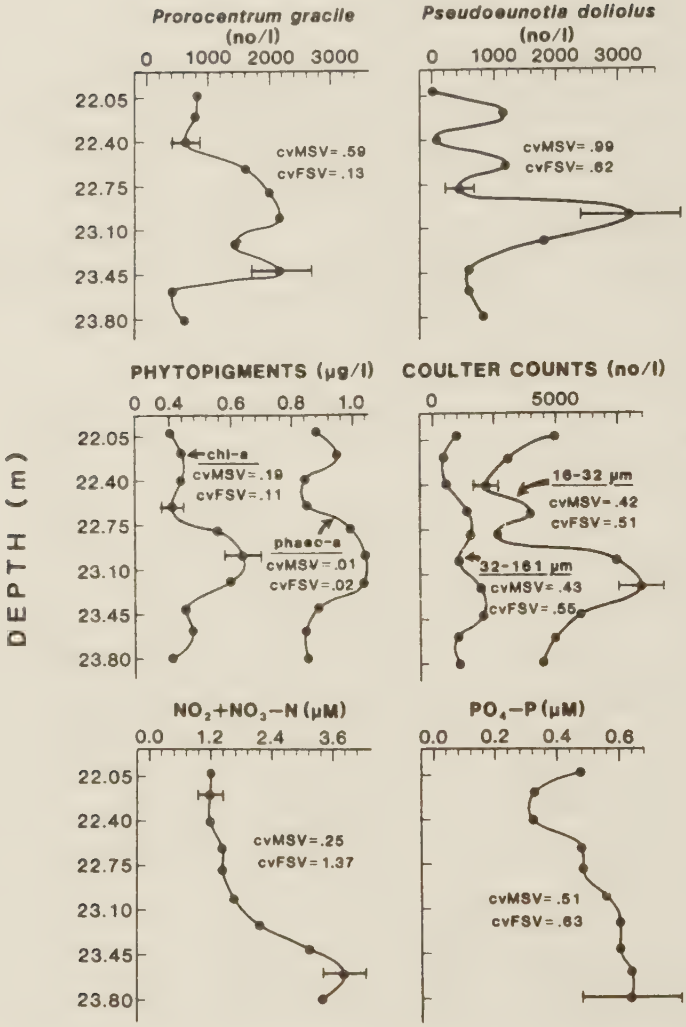

Figure 2. Profiles of organisms and environmental characteristics from a single MPS cast. Bars represent two standard deviations about the observed value.

and degree of finescale and microscale structure. The appropriate value of the error term lies somewhere between the value for duplicate and parallel sample values.

3. Results

Examples from an experience of small-scale sampling with the MPS are shown in Figure 2. This cast was made in the seasonal pycnocline at 22 m depth in 180 m of water 4 km off the California coast under calm winds and large ground swell. Similarities among profiles may be fortuitous: high correlations among populations are

Table 2. Incidence with which microscale variations (*cv-MSV*) and finescale variations (*cv-FSV*) of microplankton and environment exceeded parallel variations (*cv*-prll) and duplicate variations (*cv*-dupl) of Table 1. Values for organisms are from 29 casts. *N* is number of sets.

	Parameters of variation				
	cv-MSV		*cv-FSV*		
Characteristic	>*cv*-prll	>*cv*-dupl	>*cv*-prll	>*cv*-dupl	*N*
Organisms	61%	92%	53%	80%	471
Chlorophyll *a*	55%	71%	61%	76%	49
Phaeopigment *a*	20%	20%	45%	39%	49
Coulter 16–160 μm	42%	100%	70%	91%	33
Coulter 32–50 μm	32%	97%	44%	94%	34
Coulter 51–160 μm	32%	100%	47%	85%	34
Nitrate + nitrite	37%	—	53%	—	19
Nitrate	14%	—	71%	—	14
Nitrite	42%	—	66%	—	12
Ammonium	71%	—	85%	—	7
Silicate	25%	—	40%	—	20
Phosphate	5%	—	22%	—	18
Salinity	17%	—	42%	—	24

not commonplace in this data set. Finescale and microscale coefficients of variation are given to provide a sense of correspondence with actual concentration profiles.

Despite the more energetic mixing conditions observed off Perú, there is no evidence that small-scale variations were different from those off California. Cast means and standard deviations of Perú cast variation coefficients (*cv-MSV*, *cv-FSV*) are indistinguishable from those drawn from similar site and cast environments off California. Results of Perú and California MPS casts are therefore pooled with the caveat that the seven Perú casts, all made in austral spring on the Chimbote shelf and slope, probably under-represent the range of conditions to be found there.

a. Incidence and intensity of patchiness. The incidence with which coefficients of variation for smallscale patchiness exceeded the corresponding *cv*'s from parallel samples and from duplicate determinations is shown in Table 2, which indicates the rather commonplace occurrence of finescale and microscale structure of plankton populations and of their environment. By this criterion, concentration variations of one or more organism populations occurred in virtually all casts. Conversely, there were no casts in which every population or environmental characteristic showed high variation.

The incidence and degree of variations of organism concentrations and of environmental characteristics encountered in all 65 casts is given in Figures 3–10. Ratios of

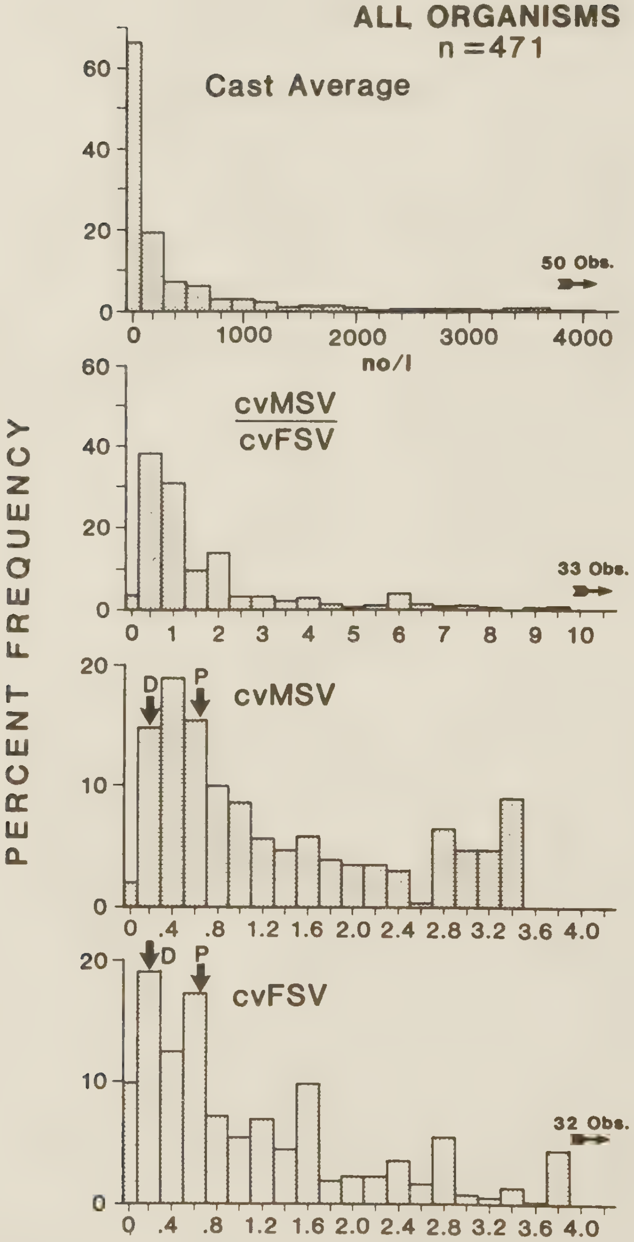

Figure 3. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for 471 organism populations in 29 MPS casts. Values for *cv*'s of determination (D) and parallel sampling (P) are indicated by arrows. Insets identify abscissas.

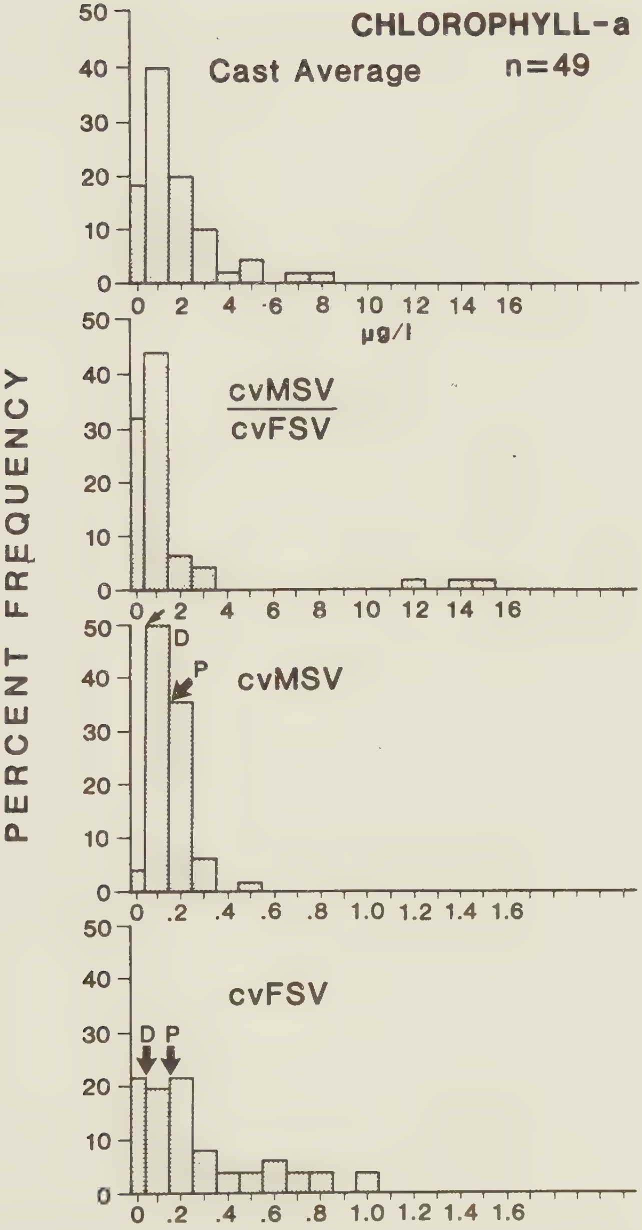

Figure 4. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for chlorophyll-*a* concentrations. Values for *cv*'s of determination (D) and parallel sampling (P) are indicated by arrows. Insets identify abscissas.

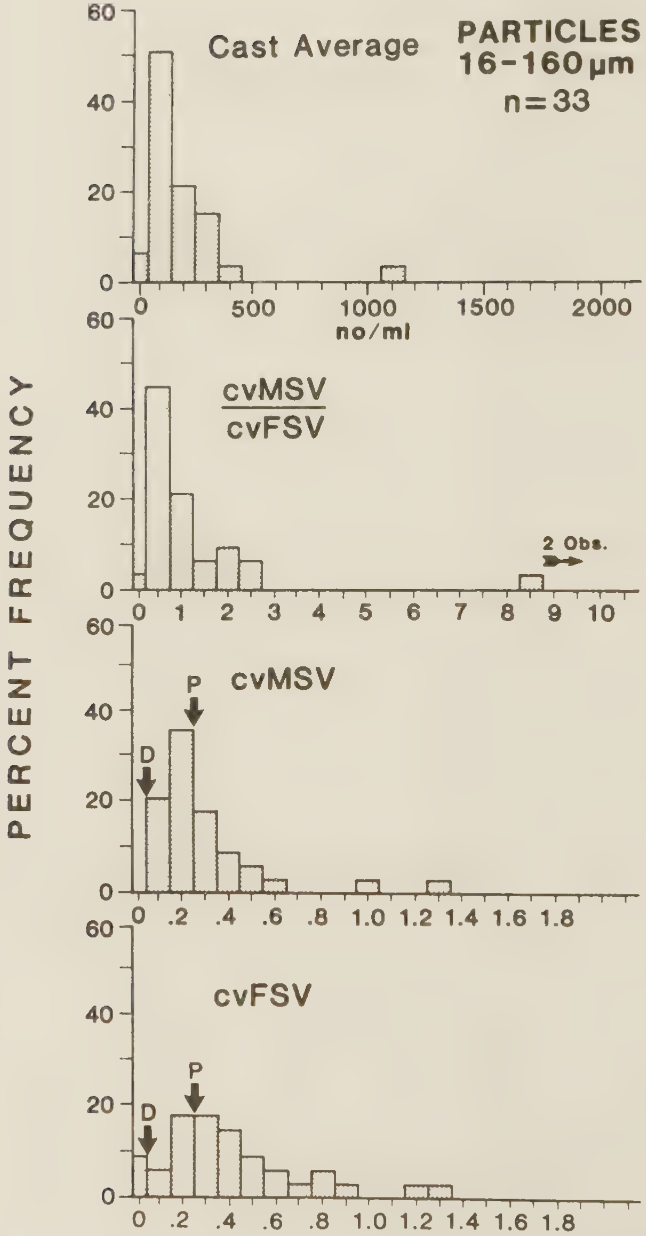

Figure 5. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for Coulter counts of particles 16-160 μm diameter. Values for *cv*'s of determination (D) and parallel sampling (P) are indicated by arrows. Insets identify abscissas.

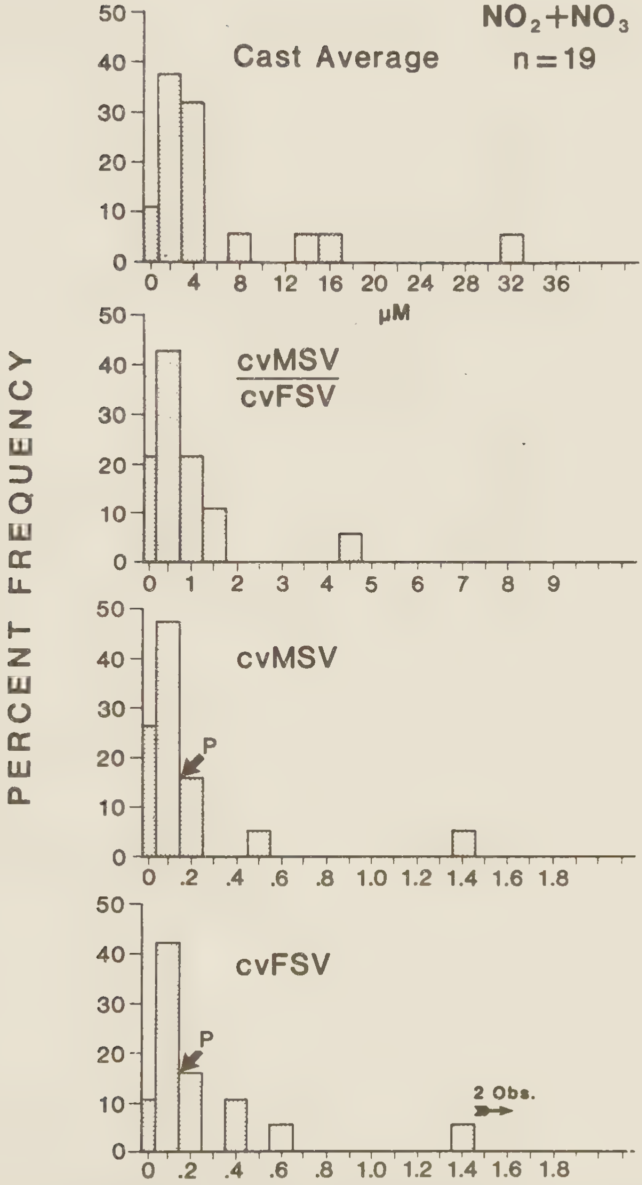

Figure 6. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for nitrate + nitrite concentrations. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

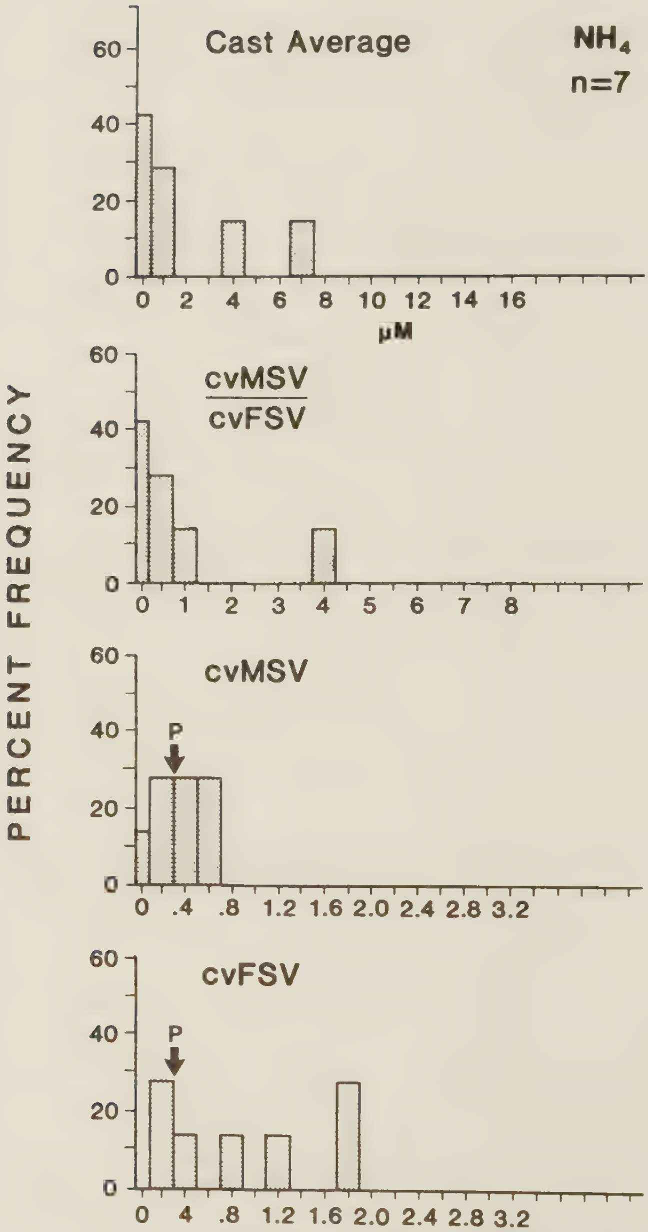

Figure 7. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for ammonium concentrations. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

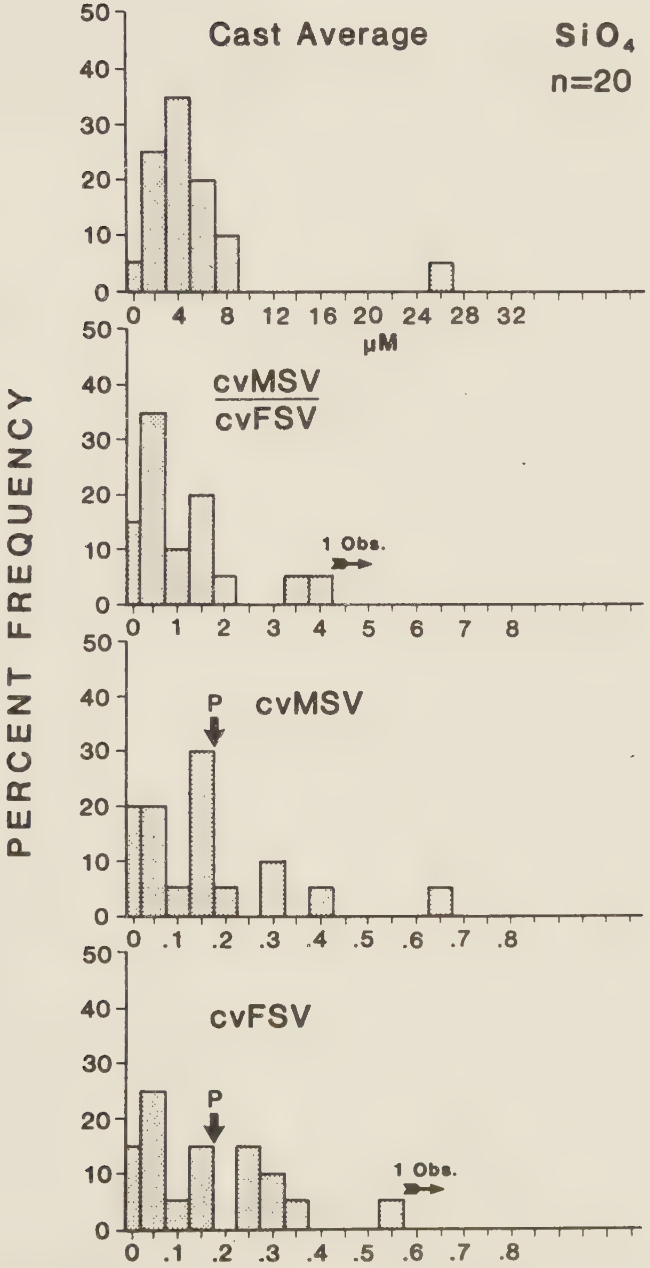

Figure 8. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for silicate concentrations. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

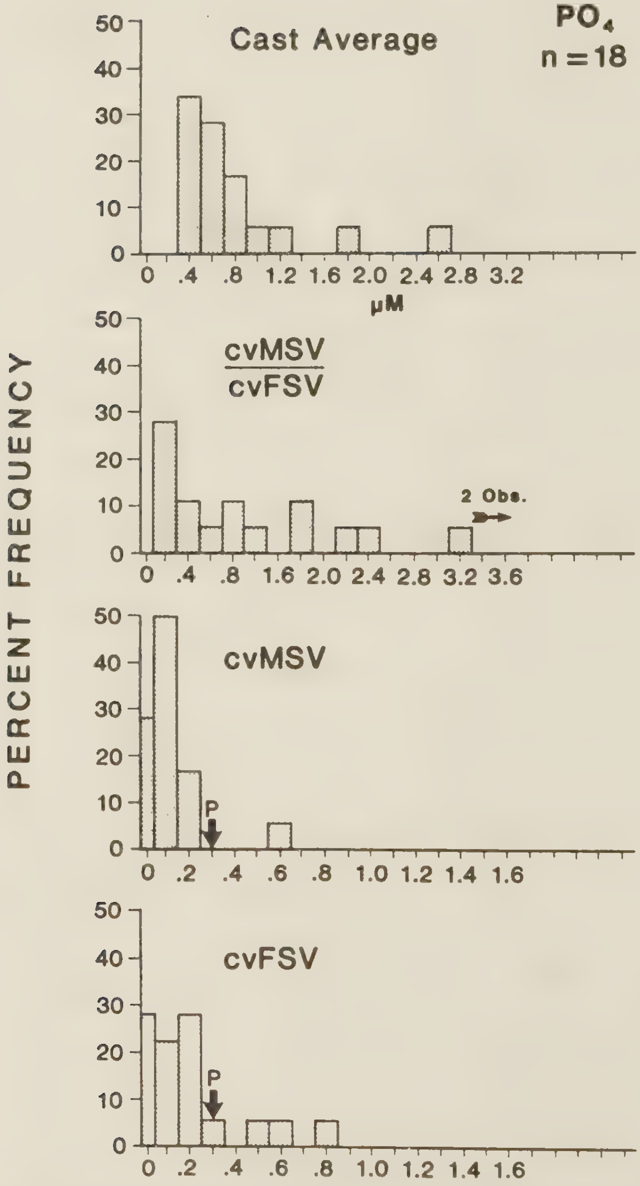

Figure 9. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for phosphate concentrations. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

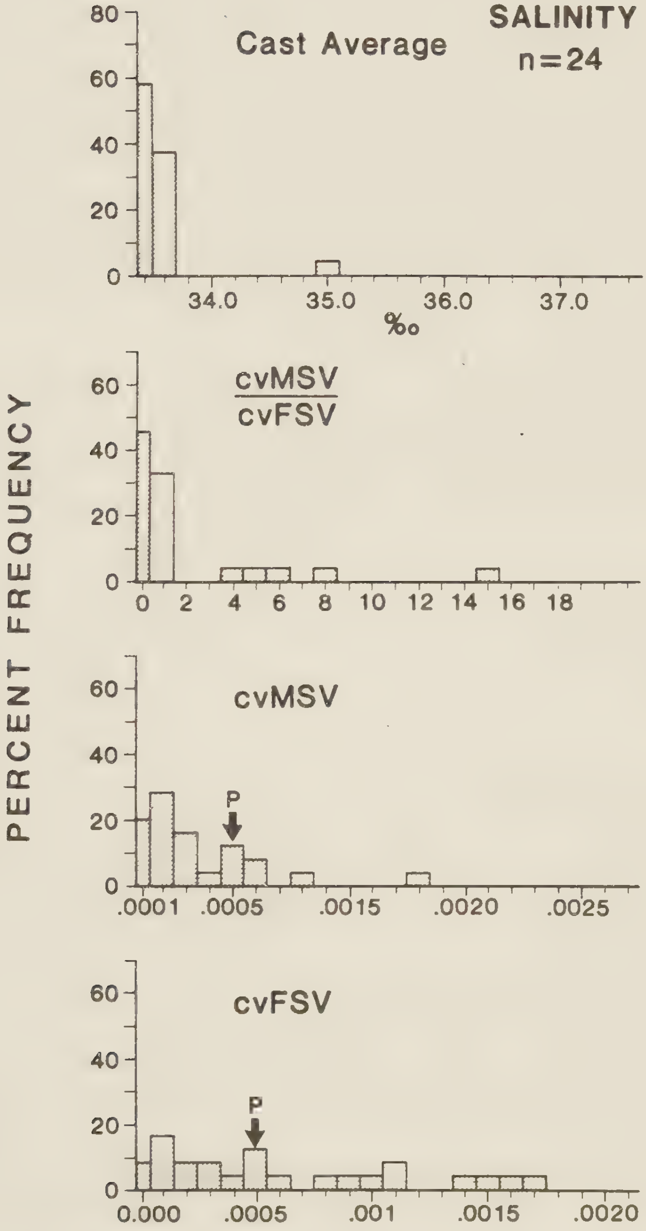

Figure 10. Frequency histograms of cast means, *cv*-ratios, *cv-MSV* and *cv-FSV* for salinities. Value for *cv* of parallel sampling (P) is indicated by arrow. Insets identify abscissas.

the variation coefficients, *cv-MSV:cv-FSV*, are shown to give a sense of the relative contribution of each to the total variation.

Figure 3 gives distributions of these parameters for every set of organism populations. The distribution of *cv*-ratios shows that microscale variation frequently exceeded the corresponding finescale variation of the same population. Distributions of microscale and finescale coefficients show that values frequently exceed twice the "error" levels.

Distributions of chlorophyll-*a* and Coulter count parameters (Figs. 4 and 5) show less variation on both microscale and finescale than those of organism populations, and more contribution to total variation from finescale gradients than from microscale patches. As discussed below, parameters for chlorophyll and particle variations reflect the effect of integration over individual population variations.

Distributions of variation parameters of nutrient species (Figs. 6–9) are comparable to those of chlorophyll and Coulter counts. Among the nutrients, ammonium showed somewhat higher incidence and degree of patchiness, silicate and phosphate showed the lowest. Nitrite patchiness was greater than that of nitrate. Finescale gradients of nutrients usually contributed more to total spatial variation than did microscale patches.

Salinity variations (Fig. 10) usually were dominated by finescale gradients. Large ratios of microscale to finescale coefficients occurred only where finescale gradients were very small. Coefficients of salinity variation are small because mean salinity is large compared with its variance.

*b. **Aliasing by organic aggregates.*** A special case of organism patchiness arises from association of organisms with macroscopic aggregates of detritus ("marine snow"), shown by Wiebe and Pomeroy (1972), Silver *et al.* (1978), and Beers *et al.* (1986), to occur for a variety of microplankton and types of snow. Such "nannoscale" discontinuities are embedded in the viscous regime dominated by Fickian (molecular) processes. This source of variation is not evaluated by sampling with the MPS because the aggregates are either small or few per liter, and are dispersed during sampling and sample processing. Associations of organisms with snow would, however, alias variational parameters if large, populated aggregates were caught by some bottles but not others. This effect could explain part of the higher variations seen between parallel samples than between duplicate determinations of organism concentration determinations.

In this data set, association of an organism population with snow would be indicated by a relationship of its concentration to detrital concentration. All five casts for which detrital particles were enumerated by microscope displayed high levels of microscale detrital variation between sample depths. Of 46 kinds of organisms enumerated among these casts, six display correlation coefficients higher than 0.5 with detritus concentration. Of the six, two appear categorically fortuitous—crustacean eggs and small post-naupliar copepods. The others are three diatoms, *Eucampia zoodiacus, Nitzschia seriata* group, *Thalassiosira* sp. *B,* and one dinoflagellate species, *Ceratium breve,* any of which have been associated with snow (op. cit.). As previously noted (Owen, 1981a), high correlations between ciliates and detritus among parallel samples in two MPS casts indicate other examples of this association.

Divers deployed to the depths of 10 daytime MPS casts off Southern California in September, 1979 estimated snow concentration at several hundred per liter, sufficiently high to denote minimal effects of uneven sampling by individual water bottles. Snow size never exceeded 3 mm equivalent spherical diameter. Variational characteristics of organisms and environmental characteristics at the dive sites were typical of those elsewhere.

c. Finescale and microscale variation by particle type. I determined patterns of finescale and microscale variation among functionally similar kinds of organisms (Table 3). To construct similar groups of organisms, I assigned each taxon to a class of trophic mode, degree of motility, and ecological relation to larval anchovy. Trophic mode classes consist of obligate heterotrophs (e.g. crustacean larvae, ciliates, *Noctiluca* and peridinnid dinoflagellates), autotrophs (diatoms and other dinoflagellates), atrophs (eggs, pollens and unidentified spheres), and detritus (strings, flakes and amorphous blobs). Motility classes consist of passives (detritus, eggs, centric diatoms), weak motiles (pennate diatoms and other forms capable of directed movements of m/dy), motiles (dinoflagellates, ciliates, crustacean nauplii, m/hr), and fast motiles (oikopleurans, small chaetognaths, small crustaceans, m/min). Larval fish interaction classes consist of prey, competitors with prey, predators, and noninteractives. "Prey" types meet the following criteria, from Rojas de Mendiola (1974) and Arthur (1976): ingestible dimensions ($20\ \mu m <$ width $< 150\ \mu m$), absence of long spines or setae, and some degree of motility (except that eggs of ingestible size are included). "Competitors with prey" are autotrophs and auto-heterotrophs other than prey, "predators" are organisms that kill fish larvae, and "inactives" are inedible atrophs and detrital substances. It must be emphasized that the "predator" category excludes larger or faster organisms that are under-represented by the collection methods by virtue of rarity or escapement ability. On the other hand, all "prey" types are capturable by the collection methods.

Aggregates of finescale and microscale coefficients for each population and cast were formed according to these rules, rather than computing coefficients for summed taxon concentrations. Even so, pooling heterogeneous populations by single attributes may have caused underestimation of patchiness differences among classes of organism attributes.

Trophism (Table 3a). Atrophs, chiefly calanoid copepod eggs, and detritus showed the least patchiness on both finescale and microscale. Autotrophs and heterotrophs showed about the same degree of finescale and microscale patchiness, well above that

Table 3. Microscale patchiness (*cv-MSV*) and finescale patchiness (*cv-FSV*) of plankton populations classified by motility, trophism and interaction with small fish larvae. *DF* is degrees of freedom, *SS* is sums of squared deviations, *MS* is mean squared deviation *SS/DF*, *F* is treatment-*MS*/error-*MS*, *N* is number of population sets in the 29 MPS casts, MEAN *cv* is mean coefficient of variation in the designated class, *STDEV* is the standard deviation of MEAN *cv*.

(a) Trophism

analysis of variance on *cv-MSV*

Source	*DF*	*SS*	*MS*	*F*	
trophism	3	25.48	8.49	7.85	$p < .001$
error	547	591.75	1.08		
total	550	617.23			

Level	*N*	MEAN *cv*	*STDEV*
autotroph	297	1.502	1.049
heterotroph	195	1.396	1.080
repro. product	37	0.918	0.921
detritus	22	0.607	0.658

analysis of variance on *cv-FSV*

Source	*DF*	*SS*	*MS*	*F*	
trophism	3	16.54	5.51	3.26	$p < .05$
error	547	925.35	1.69		
total	550	941.89			

Level	*N*	MEAN *cv*	*STDEV*
autotroph	297	1.454	1.329
heterotroph	195	1.332	1.339
repro. product	37	1.033	1.136
detritus	22	0.692	0.611

(b) Motility

analysis of variance on *cv-MSV*

Source	*DF*	*SS*	*MS*	*F*	
motility	3	5.17	1.72	1.54	$.5 > p > .2$
error	547	612.06	1.12		
total	550	617.23			

Level	*N*	MEAN *cv*	*STDEV*
passive	140	1.240	1.032
m/day	70	1.344	0.922
m/hr	296	1.452	1.098
m/min	45	1.516	1.064

Table 3. (Continued)

analysis of variance on *cv-FSV*

Source	*DF*	*SS*	*MS*	*F*
motility	3	7.64	2.55	1.49 $.5 > p > .2$
error	547	934.25	1.71	
total	550	941.89		

Level	*N*	MEAN *cv*	*STDEV*
passive	140	1.174	1.200
m/day	70	1.311	1.016
m/hr	296	1.415	1.392
m/min	45	1.557	1.440

(c) Interaction with fish larvae

analysis of variance on *cv-MSV*

Source	*DF*	*SS*	*MS*	*F*
larv. interaction	3	15.18	5.06	4.60 $p < .01$
error	547	602.04	1.10	
total	550	617.23		

Level	*N*	MEAN *cv*	*STDEV*
inactive	84	1.154	0.996
prey	220	1.280	1.063
competor	229	1.564	1.060
predator	18	1.611	0.972

analysis of variance on *cv-FSV*

Source	*DF*	*SS*	*MS*	*F*
larv. interaction	3	16.50	5.50	3.25 $p < .05$
error	547	925.38	1.69	
total	550	941.89		

Level	*N*	MEAN *cv*	*STDEV*
inactive	84	1.034	1.104
prey	220	1.306	1.340
competor	229	1.477	1.303
predator	18	1.821	1.608

of nonfeeding particulates. AOV indicated significant effects on finescale and microscale patchiness associated with trophism classification.

Motility (Table 3b). Mean values of finescale and microscale organism patchiness increased monotonically with degree of motility. Amotile and weakly motile forms such as eggs and diatoms displayed a lower degree of microscale and finescale patchiness than did faster motiles such as dinoflagellates and small crustaceans. AOV, however, indicated no significant differences between motility classes, even after combining the two faster and two slower classes.

Interaction with fish larvae (Table 3c). Populations of larval fish prey were less patchy on average than their competitors and more patchy than noninteractive forms. Predators on larvae were the most patchy. (As noted above, the "predator" category does not include larger or faster organisms that are under-represented by the collection methods by virtue of their rarity or escapement ability.) Differences in degree of patchiness were more pronounced at the microscale level than at the finescale level. Classification of microplankton by their relation to larvae pools organisms with disparate attributes, which probably minimizes statistical distinctions between categories.

d. Finescale and microscale variation by environment. To test the hypothesis that organism patchiness is related to the environment, each MPS cast was classified according to the site environment (bottom depth, mixed layer depth, wind speed and lighting at the place and time of the cast); according to the cast environment (temperature gradient, chlorophyll concentration, nutrient concentration, and Coulter particulate concentration over the 2 m interval subtended by the MPS cast); and according to the sample environment (degree of microscale variation of chlorophyll, nutrients and particulates from the MPS cast samples). Casts were grouped according to this classification and the corresponding coefficients of variation of organism populations were compared by AOV to determine environmental effects on finescale and microscale plankton patchiness (Table 4).

Chlorophyll and particulate concentrations are used here to express characteristics of the organisms' environment. Although presumably somewhat affected by the density of some types of the organisms enumerated, chlorophyll and Coulter particle measurements characterize the environment rather than organism density because they were dominated by particles smaller than those enumerated, and because detritus constituted a large fraction of particulates sensed by the Coulter counter. For these reasons, chlorophyll and particulate concentrations usually were not well correlated with concentration estimates of organisms within casts.

Because the classification treatment does not account for interaction of organism behaviors with the environment, patchiness differences in contrasting environments may be underestimated.

Effects of site environment (Table 4a). I expected finescale and microscale plankton patchiness to show the influence of processes that affect the upper 30 m of the water column. AOV was performed on finescale and microscale patch parameters at levels of light, wind, layer and bottom depth.

Microscale patchiness of organisms was significantly greater in daylight than in darkness. Possible mechanisms are diurnal variation of patchiness due to dark/light

Table 4. Microscale patchiness (*cv-MSV*) and finescale patchiness (*cv-FSV*) of organism populations by site, cast, and sample environment. *DF* is degrees of freedom, *SS* is sums of squared deviations, *MS* is mean squared deviation *SS/DF*, *F* is treatment-*MS*/error-*MS*, *N* is number of population sets in the 29 MPS casts, MEAN *cv* is mean coefficient of variation in the designated class, *STDEV* is standard deviation of MEAN *cv*.

(a) General (site) environment

Ambient lighting

analysis of variance on *cv-MSV*

Source	*DF*	*SS*	*MS*	*F*	
light	2	18.14	9.07	8.22	$p < .001$
error	578	638.09	1.10		
total	580	656.23			

Level	*N*	MEAN *cv*	*STDEV*
night	142	1.044	0.892
crepuscular	81	1.285	1.069
day	358	1.463	1.103

analysis of variance on *cv-FSV*

Source	*DF*	*SS*	*MS*	*F*	
light	2	10.13	5.06	3.02	$.1 > p > .05$
error	578	967.95	1.67		
total	580	978.08			

Level	*N*	MEAN *cv*	*STDEV*
night	142	1.078	1.169
crepuscular	81	1.430	1.454
day	358	1.371	1.303

Wind speed at 10 m above sea level

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
wind	1	13.02	13.02	11.72	$p < .002$
error	579	643.21	1.11		
total	580	656.23			

Level	*N*	MEAN *cv*	*STDEV*
<10 m/s	508	1.393	1.082
>10 m/s	73	0.941	0.834

Table 4. (Continued)

analysis of variance on *cv-FSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
wind	1	5.01	5.01	2.98	$.2 > p > .1$
error	579	973.08	1.68		
total	580	978.08			

Level	*N*	MEAN *cv*	*STDEV*
<10 m/s	508	1.343	1.318
>10 m/s	73	1.063	1.133

Mixed layer vs. pycnocline casts

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
layer	1	13.02	13.02	11.72	$p < .002$
error	579	643.21	1.11		
total	580	656.23			

Level	*N*	MEAN *cv*	*STDEV*
mixed layer	73	0.941	0.834
pycnocline	508	1.393	1.082

analysis of variance on *cv-FSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
layer	1	5.01	5.01	2.98	$.2 > p > .1$
error	579	973.08	1.68		
total	580	978.08			

Level	*N*	MEAN *cv*	*STDEV*
mixed layer	73	1.063	1.133
pycnocline	508	1.343	1.318

Bottom depth

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
bottom	2	32.98	16.49	15.29	$p < .001$
error	578	623.26	1.08		
total	580	656.23			

Level	*N*	MEAN *cv*	*STDEV*
<100 m	189	1.015	0.945
100–500 m	361	1.521	1.103
>500 m	31	1.138	0.766

Table 4. (Continued)

analysis of variance on *cv-FSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
bottom	2	17.98	8.99	5.41	$p < .01$
error	578	960.10	1.66		
total	580	978.08			

Level	*N*	MEAN *cv*	*STDEV*
<100 m	189	1.147	1.267
100-500 m	361	1.434	1.328
>500 m	31	0.821	0.884

(b) Local (cast) environment

Local vertical temperature gradient

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
temperature grad.	2	31.85	15.93	14.74	$p < .001$
error	578	624.38	1.08		
total	580	656.23			

Level	*N*	MEAN *cv*	*STDEV*
<0.1 °C/m	307	1.167	0.990
.1–.18 °C/m	159	1.340	1.064
>.18 °C/m	115	1.783	1.131

analysis of variance on *cv-FSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
temperature grad.	2	11.32	5.66	3.38	$.1 > p > .05$
error	578	966.76	1.67		
total	580	978.08			

Level	*N*	MEAN *cv*	*STDEV*
<.1 °C/m	307	1.180	1.228
.1–.18 °C/m	159	1.406	1.394
>.18 °C/m	115	1.512	1.319

Nitrate + nitrite concentration

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
ave [N]	2	22.15	11.07	9.35	$p < .001$
error	310	367.08	1.18		
total	312	389.23			

Table 4. (Continued)

Level	*N*	MEAN *cv*	*STDEV*
<2 μM	162	1.567	1.106
2–5 μM	112	1.732	1.145
>5 μM	39	0.862	0.802

analysis of variance on *cv-FSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
ave [N]	2	9.66	4.83	2.75	$.2 > p > .1$
error	310	543.79	1.75		
total	312	553.45			

Level	*N*	MEAN *cv*	*STDEV*
<2 μM	162	1.612	1.417
2–5 μM	112	1.378	1.263
>5 μM	39	1.096	1.068

Coulter particle concentration

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
ave particles	2	42.77	21.39	19.02	$p < .001$
error	281	315.92	1.12		
total	283	358.69			

Level	*N*	MEAN *cv*	*STDEV*
<70/ml	116	1.905	1.102
70–165/ml	126	1.609	1.116
>165/ml	42	0.728	0.708

analysis of variance on *cv-FSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
ave particles	2	29.39	14.70	8.56	$p < .001$
error	281	482.67	1.72		
total	283	512.06			

Level	*N*	MEAN *cv*	*STDEV*
<70/ml	116	1.642	1.345
70–165/ml	126	1.598	1.402
>165/ml	42	0.715	0.843

Table 4. (Continued)

Chlorophyll concentration

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
ave chl	2	43.16	21.58	20.15	$p < .001$
error	521	557.96	1.07		
total	523	601.12			

Level	*N*	MEAN *cv*	*STDEV*
<1 μg/l	273	1.681	1.099
1–2.5 μg/l	115	1.089	0.936
>2.5 μg/l	136	1.122	0.980

analysis of variance on *cv-FSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
ave chl	2	21.21	10.61	6.27	$p < .005$
error	521	880.85	1.69		
total	523	902.07			

Level	*N*	MEAN *cv*	*STDEV*
<1 μg/l	273	1.529	1.348
1–2.5 μg/l	115	1.033	1.090
>2.5 μg/l	136	1.267	1.363

(c) Microscale (sample) environment

nitrate + nitrite patchiness

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
cv-MSV:nitrogen	1	10.23	10.23	8.20	$p < .01$
error	282	351.79	1.25		
total	283	362.02			

Level	*N*	MEAN *cv*	*STDEV*
<.1	103	1.344	1.088
>.1	181	1.739	1.133

Coulter particle patchiness

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
cv-MSV:particles	1	37.47	37.47	32.90	$p < .001$
error	282	321.22	1.14		
total	283	358.69			

Table 4. (Continued)

Level	*N*	MEAN *cv*	*STDEV*
<.4	42	0.728	0.708
>.4	242	1.751	1.117

Chlorophyll patchiness

analysis of variance on *cv-MSV* of organisms

Source	*DF*	*SS*	*MS*	*F*	
cv-MSV:chlorophyll	1	0.70	0.70	0.61	$p > .5$
error	522	600.42	1.15		
total	523	601.12			

Level	*N*	MEAN *cv*	*STDEV*
<.15	232	1.365	1.055
>.15	292	1.439	1.086

cycles of directed organism movement or of reproduction (cf. Olson *et al.*, 1986; Chisolm, 1981). However, this result does not denote a behavioral response because, intuitively, patchiness during hours of darkness could be diminished by increased convective mixing, which would disrupt patches formed during the stabilizing period of daytime insolation.

Wind stress, which drives mixing and stirring of the upper ocean layers, similarly affects microscale variation. Wind speeds above 10 m/s (at 10 m above sea level), produced significantly less microstructure of organism populations, although wind mixing never managed to obliterate structure in mixed layer or pycnocline.

Casts in the seasonal pycnocline showed greater microstructure than casts in the mixed layer, again due to increased vertical lability of waters of the upper layer.

Casts at sites where bottom depth was less than 100 m displayed less finescale and microscale structure of organisms than did casts at deeper sites. This treatment produced the greatest separation of finescale and microscale coefficients (see *F*-ratios), perhaps because "bottom depth" is the net expression of a number of effects that operate on patchiness. Upwelling, breaking internal waves, and interaction of flow with the bottom all contribute to increased levels of vertical mixing at shallower depths, which would produce the observed result.

Effects of cast environment (Table 4b). Sources of spatial variation were expected to operate on plankton within finescale layers of the water column. AOV was performed on finescale and microscale parameters of variation to determine their sensitivity to degree of vertical stability, (estimated by the 2 m temperature gradient, grad *t*, at the cast depth), and trophic state of the water (as specified by mean concentrations of chlorophyll-*a*, Coulter particulates and nitrate + nitrite from the cast). Finescale and microscale parameters grouped according to cast environment levels show increased microscale patchiness and larger finescale gradients in more stable layers (larger thermal gradients) and in more oligotrophic layers (diminished levels of nutrients, small particles and chlorophyll). Effects on microscale variations are particularly pronounced.

Patchiness parameters follow a pattern one would expect of the influence of vertical stability on vertical exchange rates: patchiness was greater in more stable layers where contemporaneous disruption by vertical exchange was minimal.

Microscale variations of organisms were also affected by levels of nutrients, particles and phytopigment. Oligotrophic layers, those with reduced concentrations of nitrate and nitrite, particulates and chlorophyll, displayed markedly increased levels of microscale patchiness of small plankton.

Effects of sample environment (Table 4c). The microscale environment also would be expected to affect the patchiness of microplankton. Degree of microscale patchiness of the nutrient, particulate and chlorophyll fields, specified by their respective variation coefficients, accords with degree of microscale patchiness of organisms. AOV results showed microscale organism differences to be significant for nutrient and particulate patchiness but not for chlorophyll patchiness. The relationship of finescale organism parameters to microscale environment parameters is not reported because there is no reason *a priori* why microscale variation of the environment should affect the mean gradient of organisms. The accordance of organism patchiness with environmental patchiness does not necessarily denote a cause-effect condition because physical events are as likely to have given rise to both.

Environmental factors and organism characteristics considered here affect microscale patchiness more than finescale patchiness. For each determinant in Table 3 and 4, ratios of the factor mean square to the error mean square (F-values) indicate greater effects on $cv\text{-}MSV$ (the microscale coefficient) than on $cv\text{-}FSV$. Each determinant thus accounts for more of the microscale variance than of the finescale variance.

Overall, effects of environment on organism patchiness are more pronounced than are effects of intrinsic organism behaviors. This is reflected by the consistently larger mean-square ratios (F-values) throughout the environment treatments of Table 4, as compared with those of organism characteristics of Table 3. This connotes dominance of physical determinants over biological determinants of smallscale patchiness, but it may also reflect an artifact arising from pooling organisms with differing behaviors.

e. Patterns within MPS casts. Tests to determine the incidence of pattern within the 2 m cast interval were conducted. I computed serial correlations on original and detrended (residual) values of organism concentrations and of environmental characteristics using the "mean-square successive difference test" described by Zar (1974). The test statistic is

$$S = 1 - s(d)^2/s^2$$

where $s(d)^2$ is the sum of squared successive differences in concentration through a sample set divided by $2(n - 1)$, and s^2 is the variance of the sample set.

Table 5. Incidence of significant values of runs tests among original values and residuals about the mean gradient of organism and environmental concentrations within MPS casts. N is number of serial data sets tested.

Characteristic	N (sets)	Percent significant originals (95% level)	Percent significant residuals (95% level)
Organisms	607	13	5
Chlorophyll-*a*	49	33	10
Phaeopigment	49	31	6
Particles 16–160 μm	34	21	0
Particles 32–50 μm	34	18	6
Particles 51–160 μm	34	15	3
Nitrate + nitrite	18	39	17
Nitrite	11	27	9
Nitrate	13	54	23
Ammonium	16	37	6
Phosphate	6	25	0
Silicate	18	22	11
Salinity	24	39	8

The results (Table 5) indicate a low incidence of significant serial correlations among organism populations (13% for originals and 5% for residuals). Thus organism patch sizes usually were at or below the interval sampled by the MPS, i.e. less than 2 m. The incidence of significant serial correlations among original values of all environmental characteristics was higher than that among organism populations. In 285 sets of environmental characteristics, S-values were significant in 30% of the original sequences. Finescale gradients were more common among environmental variables than among organism populations, indicating that environmental characteristics were often arranged in gradients greater than 2 m in vertical extent. Among residual series of the environmental concentrations, the incidence of significant S-values was higher for nitrate, silicate and chlorophyll, indicating a somewhat coarser submeter scale of patchiness among these than among organisms or other environmental characteristics.

f. Patch intensity and size. Manipulation of the small-structure parameters reveals some characteristics of dimension and intensity of organism patchiness. As shown by Lloyd (1967), the nondimensional contagion parameter, k, of the negative binomial distribution expresses the reciprocal proportion by which mean crowding, c^*, exceeds mean concentration, $\bar{c}$, over a defined domain:

$$c^*/\bar{c} = 1 + 1/k.$$

Mean crowding and the k-parameter were computed for each population in each MPS cast from the organism concentration files. The k-parameter is related to the unpartitioned coefficient of variation (over the entire cast) by the equation

$$k = 1/(cv^2 - 1/\bar{c}). \tag{1}$$

Small k values thus imply patchiness, and large values imply random distributions. Values for k range from 0.097 ($c^*/\bar{c} = 11.3$) to 301 ($c^*/\bar{c} = 1$) among 552 records; the median value is 1.031 ($c^*/\bar{c} = 1.97$). Lloyd's expression above approximately gives the relationship of concentration in patches to mean concentration. The median value suggests that patch concentrations most commonly are twice the mean concentration. The range over all records suggests that patch concentrations can exceed mean concentrations by more than 10-fold.

The finding that microplankton populations occur in small clusters substantiates the conclusion from theory by Vlymen (1977) that prey patchiness must occur on the scale of optimum foraging strategy by anchovy at pre-schooling larval stages.

Vlymen (1977) gives expressions from which patch geometry and frequency can be derived. Using the median value in Vlymen's expression (his Eq. 23) for patch size, k and mean concentration in this data set yields geometric patch diameters of 4 cm at organism concentrations of 5/ml, and 12 cm at 50/ml. The median patch size was 27 cm. Corresponding inter-patch distances, computed from Vlymen's Eq. 24, were 8 cm and 15 cm, respectively.

Patchiness at submeter intervals appears frequently to attain the optimum intensity ($c^*/\bar{c} = 11$) for larval anchovy feeding that is derivable from Vlymen's model: eighteen percent of all microplankton populations fell between $c^*/\bar{c} = 10.5$ to 11.3. This model was based on food densities used to sustain laboratory-reared larvae: because larvae may require more food in tanks than in the sea, the incidence at sea of adequate food concentrations may be higher than that derived from the model.

g. Simulations of patchiness. The experiences of sampling on the submeter scale are summarized by vertical sections of concentrations of a hypothetical microplankton population (Fig. 11). The figure portrays the sensitivity of microscale patchinesss to wind, an easily monitored parameter of the mixing environment: patchiness is comparably sensitive to vertical stability and to the diurnal convection cycle. The cut-off wind speed value of 10 m/s represents the onset of turbulent vertical mixing (Simpson and Dickey, 1981).

Organism concentration fields portrayed in Figure 11 were simulated from negative binomial distributions, each with a mean value of 100 organisms/1 and with contagion parameters derived from Table 4a through Eq. 1 for microscale patchiness under low and high wind conditions. Finescale gradients are not represented. Horizontal scale of patchiness is assumed to be four times that of the vertical. This ratio is based on mean ratios of patchiness coefficients of organism populations and environmentals from four

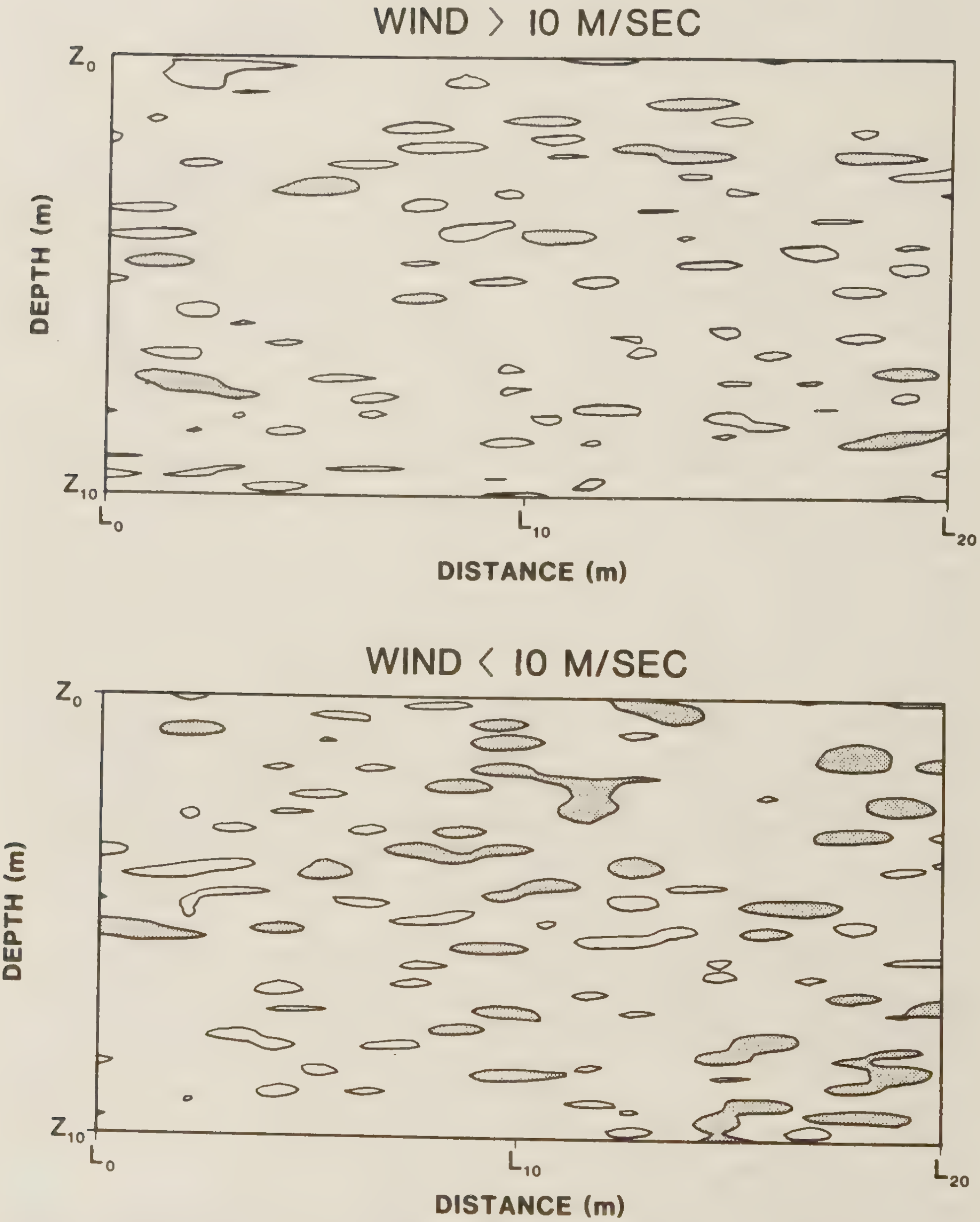

Figure 11. Vertical sections of microscale organism patchiness simulated under contrasting conditions of wind speed. Contours delimit zones where organism concentrations exceeded twice the mean value. Shading denotes zones where maximum concentrations exceeded four times the mean value.

Table 6. Individual and aggregate population statistics for microscale coefficients of variation (*cv-MSV*) in all MPS casts. Summed populations, chlorophyll-*a* and particulates represent aggregate characteristics. *cv*-error values are from Tables 1 and 2. *N* is number of data sets used.

	N	Mean	S.D.	Min.	Max.	*cv*-error
Individual populations	522	1.39	1.06	0.08	3.35	.22
Summed populations	29	0.26	0.15	0.06	0.14	.22
Chlorophyll-*a*	49	0.14	0.08	0.03	0.46	.08
Particulates 16–160 μm	33	0.30	0.25	0.08	1.32	.06

pairs of horizontal and vertical casts and is in close agreement with corresponding ratios of smallscale chlorophyll variations measured *in situ* by Derenbach *et al.*, 1979.

In these simulations (Fig. 11), patch incidence is no higher at low wind speeds: the number of patches is about the same under high and low winds. Patch intensity, however, is markedly affected: patches under low winds are larger and contain more organisms.

Also apparent from these simulations is the improbability either of representing typical concentrations or of detecting extreme concentrations from point sampling of the water column at large intervals. Integrative sampling by net hauls or pumping water is equally unlikely to yield more than rough estimates of the average concentration. Average concentration, however, has virtually no meaning to predators, which experience wide deviations from average feeding conditions over short distances.

h. Population aggregates and concentration dependence. Early explorations of organism population data failed to reveal any consistent relationships among population concentrations within MPS casts. This indicated that populations had disjoint distributions at finescale and microscale dimensions, and that small foragers encounter a variable selection of prey types in their ambits over short distances.

Whereas individual populations frequently exhibit finescale and microscale patchiness, in the aggregate they do not. The evidence for this lies in comparison of coefficients of variation from individual population concentrations with coefficients from measures of aggregate concentrations, i.e. summed populations, chlorophyll and Coulter particle counts (Table 6). The mean coefficient of variation of individual populations exceeds five times that of summed populations, nine times that of chlorophyll concentration, and over four times that of Coulter particulate concentration.

Whether by physical or biological means, the microplankton community more completely occupies available space in the water column than any of its constituent populations. Thus microhabitat spaces appear to be occupied by a variety of partially segregated population patches. Partitioning of the living space is thus denoted which may operate to the advantage of all populations present. This would increase the capacity for kinds of organisms to co-occur. As stated by Richerson *et al.* (1970), the biological system exhibits a state of contemporaneous disequilibrium.

Microscale partitioning of the habitat could be related to population densities. Concentration dependence would be expected to occur when population members are competing, even temporarily, for local resources. To test the hypothesis that higher population concentrations produce increased patchiness, I regressed mean concentrations of each population (independent variable) against the square root of respective values of the population's micro- and finescale parameters, MSV and FSV. Expressions for the relationships are:

$$\sqrt{MSV} = \text{rms(microscale)} = -9.8 + .344\,\bar{c}$$

$$\sqrt{FSV} = \text{rms(finescale)} = -181 + .339\,\bar{c}$$

where $\bar{c}$ is mean concentration in no/1. Microscale patchiness was positively dependent on mean population concentration ($r^2 = 0.92$). A lower degree of concentration dependence was shown for finescale variation ($r^2 = 0.70$).

4. Mechanisms and ecological consequences

Because a variety of processes may evoke finescale and microscale plankton distributions, it is useful to consider which are the more likely to be responsible and how they affect microplankton and predators.

a. Sources of patchiness. Organism characteristics can determine larger-scale vertical patterns (Cullen and Eppley, 1981). There is evidence from the present data treatments that reproduction dominates over motility in its influence on patchiness at small scales. Mean patchiness levels increase with organisms' motility level (Table 4b) but patchiness differences are not statistically significant ($p > 0.2$). By contrast, patchiness differences among trophic classes of populations are significant ($p < 0.05$, Table 4a). The latter separation is due mainly to patchiness differences between atrophs and feeders (autotrophs and heterotrophs), with atrophs displaying less patchiness (Table 4a). Atrophs have no motility ("passives" in Table 4b) and no reproductive capability. If differences in patchiness between atrophs and feeders are not due to differences in motility (Table 4b), perhaps they are due to differences in reproductive capacity.

Microstructure of biological particles more clearly reflects recent or current events of mixing and stirring. The conclusion of Frontier (1978–1979) for larger plankton and scales of sampling, that the mean statistics of plankton abundance correspond with the statistics of passive particles suspended in a turbulent medium, may thus extend to submeter scales for small plankton. The physical controls of plankton patchiness at scales upward of 10 m, reviewed by Denman and Powell (1984), are here extended to dimensions in the inertial subrange (ca. 0.1 m to 1 m), the transition regime between the buoyancy and viscous domains (cf. Mackas *et al.*, 1985).

Energy for mechanically redistributing plankton on small scales arises from a variety of sources, including shear and internal wave instability, wind stress, free vertical convection, lateral thermohaline intrusion and salt fingering.

Shear instability—Billow turbulence events attributed to Kelvin-Helmholtz instabilities have been detected in the upper layers of the seas and apparently are commonplace. Signatures of billow turbulence have been observed directly from the behavior of dye layers on sheets of submeter vertical extent in the seasonal thermocline (Woods and Fosberry, 1967; Woods, 1968a), and indirectly from high-resolution thermal profiles in the main and seasonal thermocline, which display zones of large temperature variations on submeter scales (Wiley, 1972; Gregg, 1980 and references therein; Gallagher, 1976; Hogg *et al.*, 1978). A current discussion concerns whether such signatures are relicts of rare, powerful events (Gibson, 1982), or whether they represent frequent, contemporaneous events in the upper thermocline (Gregg, 1980).

A current hypothesis holds that mixing in the interior of the ocean is dominated by internal waves (Garrett and Munk; 1972, 1975): at critical values of the shear forces, internal waves break and generate turbulence that is detectable by perturbations of the vertical temperature gradient. Measurements of these signatures have shown that mixing events are not random but occur in patches of high activity that vary from centimeters to tens of meters in vertical extent (e.g. Gregg, 1980). Smaller patches are the more common. According to theory and observation, such patches are more likely to occur at preferred sites that are definable from the internal wave field and vertical stability.

Several reports suggest that physical variations of small vertical extent can be laterally coherent for hundreds of meters and temporally coherent for hours to days (e.g. Woods and Fosberry, 1967; Simpson, 1971; Osborn and Cox, 1972; Kullenberg, 1974—at <100 m depth; Williams, 1976—deeper). Others suggest that this is usually not the case (e.g. Gargett, 1975; Hayes, 1975), that such signatures are more highly intermittent in space and time. Persistence and extent of the physical signatures of turbulence thus are probably variable. The existence of such signatures, however, suggests that other substances, including small plankton redistributed by the same turbulent events, may also exhibit similar lateral coherence for periods that would depend on the organism's behavior.

The attenuation of microscale plankton patchiness where sea floor depths are less than 100 m (cf. Table 4a) may reflect the higher incidence of billow turbulence on the continental borderland as incoming internal waves encounter either the bottom or the relatively destratified waters above the shelf.

Salt fingering—Local sources of microscale turbulence at ocean mid-depths include double diffusion (salt fingering), which occurs across pronounced vertical decreases in salinity. CTD profiles, taken at most MPS sites, exhibited low salinity gradients (0.33‰ in 10 m was maximum), and MPS-sampled salinity differences in 24 MPS casts never exceeded 0.055‰ in 2 m or 0.023‰ in 20 cm. In the absence of strong vertical gradients of salinity and of temperature inversions in the regions of concern here, salt fingering alone is unlikely to produce signatures that dominate over shear-induced sources of variation.

Lateral intrusions—Thermohaline intrusions, on the other hand, commonly occur in the regions sampled for plankton microstructure (Reid, *et al.*, 1958; Gregg, 1975; Johnson *et al.*, 1978). Dissipation of kinetic energy was found by Gregg to be particularly high at boundaries of intrusion zones off Baja California, and due to intense fluctuations at submeter scales. Johnson *et al.*, working with finescale CTD records, concluded that wave-induced vertical straining dominated over thermohaline intrusion to determine finestructure. Records from CTD profiles at most MPS cast sites show evidence of shallow intrusions with thicknesses greater than 5 m, usually at depths below the seasonal pycnocline. Within the 1 m limit of depth resolution of these CTD casts there was seldom any indication of intrusions of small vertical extent. Although direct effects on organism patchiness by smallscale intrusions are discounted, fluctuations associated with intrusions in the buoyancy subrange may have affected smallscale patchiness.

Surface sources—Wind stress and convective mixing transfer surface-generated momentum to deeper layers and destroy solar-induced gradients in the mixed layer or, at higher rates, erode and deepen the seasonal thermocline (e.g. Price *et al.*, 1986; Denman and Gargett, 1988). Yet they may or may not destroy larger-scale discontinuities in plankton concentrations. For example, Lasker (1975) documents the [Eulerian] disappearance of the main chlorophyll maximum layer with the passage of a storm off Southern California, whereas Mullin *et al.* (1985) describe the preservation of vertical stratification of plankton with the passage of another storm. At yet smaller scales, Owen (1981b) describes the persistence of plankton microstructure in the face of windy conditions at the continental shelf-break off Perú.

Microscale variation of small plankton decreases with increasing wind stress unless sheltered by local temperature gradients (Table 4a,b). As seen in day-night differences (Table 4a), microscale variation also decreases with the increased convective mixing that ensues during darkness, as reported by Woods (1968b). On the other hand, microstructure was not obliterated even at the highest mixing conditions encountered, whereas finescale variation was not detectably different under the various mixing regimes.

It is likely that genesis and exodus of plankton patches parallel the cascade of turbulent energy from larger to smaller scales. In other words, large patches, formed for example by baroclinic instabilities, are milled into progressively smaller patches as stirring proceeds by flow irregularities of smaller scale. At some scale smaller than that of concern here, patchiness must become isotropic and then disappear.

b. Ecological implications. This work suggests that physical forcing of population and community characteristics operates through its influence on plankton patchiness. Microplankton patch incidence and intensity are sensitive to physical mixing processes in the turbulent domain. The presence of microplankton patches alters interactions among individuals and populations; e.g., small planktivores, which depend on rate of prey encounter, are more likely to survive and grow where their food rations are patchy on the scale of their foraging ambits because the prey menu and rations available are enhanced at higher incidence and intensity of patchiness. Widespread effects on predator populations are possible because large areas suitable for survival of small predators can be created or deleted by large-scale processes that determine microscale patchiness. Community characteristics are altered in ways depending on whether strongly dominant populations emerge from vigorously mixed environments or whether competing populations co-exist in higher numbers and diversity by virtue of a minutely structured living space.

Processes of formation and maintenance of microscale patchiness are likely to affect mortality and growth of larval fishes, and must be included in our perception of factors governing their well-being. One body of evidence suggests that foraging, even by smaller organisms in the sea, is highly episodic and of limited duration. Despite the widely held view that pelagic fish larvae need high densities of microplankton (e.g. Vlymen, 1977; Lasker and Zweifel, 1978; Houde and Schekter, 1978; Lasker, 1978), transience in the co-occurrence of fish larvae and their prey has been noted at larger scales by Govoni *et al.* (1985) for sciaenid larvae, by Fortier and Leggett (1984) for capelin larvae, and by Arthur (1976), O'Connell (1980), Methot (1981), and Brewer and Kleppel (1986) for anchovy larvae. This transience may be due to infrequency of encounters of predators with prey patches if patches are ephemeral or widely spaced. More likely, the coincidence of predators with prey patches is underdocumented because it mostly occurs on small scales: prey patches are most often small, and special circumstances or new methods are needed to detect their co-occurrence in time and space.

Whether fish larvae seek or otherwise respond to prey patches in the natural habitat is thus unanswerable at present. An indication that they may is furnished by Hunter and Thomas (1974), who describe laboratory observations of a behavioral mechanism whereby larvae remain longer in small patches of higher food concentration: larvae swim shorter distances and turn more frequently in zones with larger numbers of strike targets. By this mechanism, larvae would collect in prey patches even in the absence of directed movement of larvae to a patch.

c. Resource management implications. Finescale and microscale patchiness of biological materials can be indexed from a combination of easily monitored physical and biological field values over larger domains than could ever be surveyed directly. This would satisfy a current need for assessing the incidence and intensity of plankton patchiness to specify regions and periods of adequate foraging conditions for larval fishes over the entire time-space domain of adult fish spawning. An indication of the power of such an approach to fishery management is provided collectively by Peterman and Bradford (1987), Wroblewski (1984) and Vlymen (1977). These works addressed Lasker's (1975) hypothesis that wind mixing dissipates the large-scale chlorophyll maximum layer where prey is more abundant on average, leading to increased mortality of fish larvae by starvation. Peterman and Bradford concluded that timing, intensity and duration of wind mixing events accounted for most of the interannual variations of mortality rates of anchovy larvae, more than offshore transport or cannibalism by adults. Wroblewski concluded that the lowest mortality of anchovy larvae must occur in prey patches, and Vlymen concluded that such patches were necessarily small. Together with this paper, these works provide a basis for regional specification of anchovy survival from environmental effects at the microscale.

5. Summary

Whereas feeding conditions for small predators in the sea often appear subsustaining on average, zones of a meter or less usually exist where microplankton concentrations are much above (and much below) average. According to field sampling results, small predators moving two meters vertically are 95% likely to encounter noncolonial microplankton populations that range 240% above or below their average concentration in the seasonal pycnocline and 144% above or below their average in the upper mixed layer. Such patchiness depends upon levels of wind mixing, ambient lighting, local temperature gradient and oligotrophy, and upon the microscale environment. Less clearly, microplankton patchiness depends upon organisms' reproduction capacity and population density. Population patches are spatially disjoint: thus the menu of small predators is more diverse and, whether by physical or biological means, the microplankton community more completely occupies available space than its constituent populations in a biological system that exhibits a state of contemporaneous disequilibrium.

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8948

Spawning and Survival Patterns of Larval Northern Anchovy, *Engraulis mordax*, in Contrasting Environments—A Site-Intensive Study

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J. R. Hunter, and Y. Watanabe

ABSTRACT: During the 1985 spawning season of the northern anchovy, *Engraulis mordax* Girard, off southern California, a serial field study at contrasting sites linked measurable environmental characteristics with parameters of larval anchovy growth and survival and determined a range of environmental conditions over which northern anchovy had recently spawned. Surface and water column characteristics were measured while following surface drifters at each site, and their relation to corresponding measurements of larval anchovy production, growth, mortality, and starvation are reported.

The nearshore site was eutrophic with low current speeds, low wind speeds, and high forage levels which are characteristic of coastal spawning areas. The offshore site, by contrast, was relatively oligotrophic and had higher surface mixing rates, a deeper mixed layer, reduced stability in the pycnocline, and lower forage levels.

Among the measured characteristics of the ichthyoplankton, only one, the larval production rate, was markedly different at the two sites. Although habitat suitability for adult anchovies was different, survival probability for larval anchovies was more equivalent at the two sites than inspection of single parameters of the environment suggested. In contrast with the view that the northern anchovy spawns indiscriminately, the results of this study suggest that components of the adult northern anchovy population tend to spawn under conditions and at levels that yield consistent survival probabilities for their offspring.

Since Lasker's (1975, 1978, 1981) pioneering work on causes of larval fish mortality, recent developments have made techniques available to assess age-specific larval growth, mortality, and physiological condition. These developments have piqued interest in field studies that link environmental processes to survival probabilities for larvae of broadcast spawners. Here we present the results of a site-intensive shipboard study that combined newly available measures of larval condition with a suite of physical and biotic measures of their environment in the Lagrangian setting provided by near-surface drifters to determine local variations of a few days duration. Our results are intended to guide the design and execution of programs that address the recruitment process and its relation to the spawning environment.

Conditions under which northern anchovy, *Engraulis mordax* Girard, spawn and under which their eggs and larvae survive presently are known mainly from cruises of the CalCOFI program, which are quasi-synoptic surveys of broad areas of the spawning domain during which limited sets of environmental observations and measurements have been made (cf. Reid 1988). Owing to limits imposed by time and resources, such surveys do not yield knowledge of the local fate of spawned products because the methods that characterize survival likelihood of larval fish have only recently been developed and verified, and because local changes (those embedded in the surface flow) are not knowable by the survey approach.

METHODS

Site Selection

Criteria for selection of the two study sites were that each must 1) show evidence of recent spawning by anchovy, 2) contrast with the other site in macroscopic setting and environmental character, and 3) exhibit no local gradients indicative of smaller scale (0.1–10 km) environmental

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heterogeneity. The study followed a routine survey by the California Cooperative Fisheries Investigations (CalCOFI Cruise 8502) of the northern anchovy spawning domain. Visual inspection of plankton catches made on this survey yielded estimates of northern anchovy egg abundance at 4–10 nmi intervals. Within areas of high egg abundance, the ship's survey records of 3 m temperature and in vivo phytoplankton pigment fluorescence were scanned for evidence of local gradients. Low variations of pigments and temperature in the vicinity of possible sites were verified by inspection of available satellite images of sea surface temperature and surface layer color, and several sites were then targeted for this study.

At sea, we verified that our criteria held at each site by inspection of plankton tows to confirm recent (and therefore sustained) spawning activity, and by inspection of underway records for local homogeneity of temperature and pigment fluorescence at 3 m depth. We occupied sites shown in Figure 1.

Procedures on Site

Upon verification that a site met the three criteria, we launched a radio-transmitting surface drifter. The ship then moved several nmi to launch a second drifter. Thereafter, we alternated our station pattern between the two drifters, locating each drifter by radio direction-finding equipment and visually. Each site was thus defined, in the Lagrangian sense, to be the water corpus that was moving along with the two drifters. We assumed that both drifters at each site were implanted in macroscopically homogeneous water with respect to physical and biological character. We examine the limits of this assumption by contrasting variations within and between drifters at the same site.

Stations were patterned around each drifter, in turn, at cardinal points 2 km from the drifter. Vertical plankton tows, "CalVETs" (Smith et al. 1985), were made with 150 μm mesh nets from 50 m depth at all four stations to catch fish eggs and larvae to determine age-specific anchovy production and mortality. Oblique bongo tows were made to and from 50 m depth with 333 μm mesh nets and, after we lost the 333 μm mesh nets, with 505 μm mesh nets to catch northern anchovy larvae for estimation of starvation incidence and recent growth rate. At two of the four stations, paired vertical tows similar to CalVETs were made from 50 m depth with 75 μm mesh and 333 μm mesh nets to estimate composition and quantity of larval food rations and of other small plankton, respectively. CTD/Niskin casts were made to 100 m depth at one station, per drifter visit, to measure physical structure of the water column and to get water samples at 10 depths to determine concentrations of particulates, chlorophyll-a and phaeopigments. Secchi depth was determined at one station (daylight permitting) at each drifter to estimate thickness of the euphotic layer. Standard weather observations were made once per drifter visit.

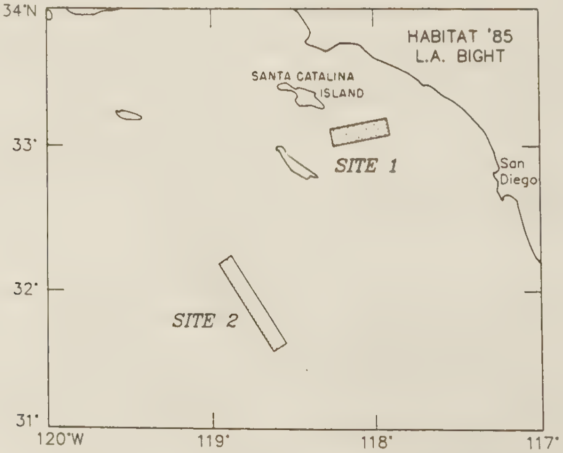

FIGURE 1.—Study site locations in the Southern California Bight.

Environmental Characteristics

Surface Drift

Drifter positions were determined by a combination of satellite navigation, Loran-C, and Decca radar over the course of the study, and were precise within 0.1 km. The drifters were designed as described by Davis et al. (1982) to minimize the effects of wave motion and of wind drag on exposed surfaces, both of which cause deviations of drifter motion from that of water parcels. The 2 km station spacing around each drifter was large compared with precision of drifter position and with deviation of the drifter's motion from surrounding water motion.

Vertical Temperature and Salinity Profiles

Temperature, conductivity, and pressure were recorded with a Neil Brown CTD, following methods used by NOAA/Southwest Fisheries Center.[1] Briefly, 0.25 s scans of temperature, conductivity, and pressure were recorded as the CTD profiled at 20–40 m/min. Conductivity and temperature records corrected for temperature lags are smoothed by a 5–point weighted running mean with binomial coefficients of 1, 4, 6, 4, 1. Salinity was computed using the Practical Salinity Scale of 1978. Salinities and temperature were compared and justified with salinity and temperature values from a hydrographic bottle tripped in the near-surface layer during each cast. Final data were enumerated at 2 m depth intervals.

Phytoplankton Pigments

Chlorophyll-a and phaeopigment-a concentrations were determined from fluorescence readings on a Turner 111[2] Fluorometer before and after acidification of 24 h extractions in 90% aqueous acetone of material retained on Whatman GF/C glass filters after filtration of 140 mL water samples.

Particles

Particle concentration and size distribution (16–160 μm equivalent diameters) were determined with a Coulter model Ta counter with a 280 μm pore configured to count particles in a 20–200 mL sample volume. Counts usually exceeded 40,000 per sample. These determinations stopped part way through the study owing to equipment malfunction at the second site.

Microplankton

Microplankton samples were aliquoted prior to counting. A 0.5 mL Stempel pipette was used 10–40 times to withdraw a subsample from the well-stirred original sample after adjusting the original volume to 750 mL. When 10 Stempel subsamples yielded too many plankters to enumerate, the sample was divided with a Folsom splitter to yield a countable fraction from at least 10 Stempel subsamplings.

Microplankton samples were enumerated in covered chambers with a Wild dissection microscope (at 250 magnification) to determine mean concentrations of larval anchovy food organisms in the upper 50 m. Food organisms are here assumed to be those having ingestible dimensions (20–160 μm width), no pronounced spines or processes that would interfere with ingestion or with gut wall integrity, and, except for ingestible eggs, some degree of motility (Rojas de Mendiola 1974; Arthur 1976). Food concentrations and rations given here are underestimated because larvae are known to take organisms smaller than were retained by the meshes of the 75 μm mesh net used (Rojas de Mendiola 1974; Arthur 1976). The sampled food fraction probably represents the major part of available food rations; although less in number, this fraction is greater in volume than the unfiltered fraction and is captured selectively by larvae (Lasker and Zweifel 1978; Theilacker and Dorsey 1980). The food retained by the net is assumed here to be the majority of, and proportional to, the total rations available to larvae over the 50 m layer sampled.

Zooplankton

Zooplankton counts were made on all organisms collected in the 333 μm mesh vertical tows. Samples were not aliquoted. The net tow method used precluded quantitative representation of faster or rarer organisms, including some types of potential predators on fish larvae. Determined for each sample were number of species, number of specimens of each species, and sex ratios (where applicable) for the following major taxonomic groups: Medusae, Siphonophorae, Ctenophora, Chaetognatha, Cladocera, Ostracoda, Amphipoda, Copepoda, Euphausiidae, crustacean larvae, other invertebrate larvae, pelagic Mollusca, Polychaeta, Tunicata, Radiolaria, and Foraminifera. Anchovy eggs and larvae, sized to the nearest 0.25 mm, were also enumerated from these collections. Zooplankton enumerations are given in detail in Alvariño and Kimbrell (1987).

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[1] K. Bliss, Oceanographer, Southwest Fisheries Center, La Jolla, CA, 92038, pers. commun. May 1985.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Larval Characteristics

Larval Growth

Growth of larvae was estimated from 224 larvae collected in 15 tows at Site 1 and from 116 larvae collected in 30 tows at Site 2. Samples for otolith ageing of larval anchovies were taken from the portside net of bongo tows and were preserved after removal of gelatinous zooplankters in 80% ethanol buffered with 20 mM tris [hydroxymethyl] aminomethane. Larvae were sorted from the plankton and stored in the same preservative.

Standard lengths of larvae were measured prior to removal of their otoliths. Preserved standard lengths were converted to live lengths using a correction factor for net shrinkage (Theilacker 1980). At Site 1, tow duration was six minutes and each sample was fixed within five minutes of tow completion. Length of the inshore larvae were corrected by a net shrinkage factor of eight minutes. Tow duration at Site 2 was also six minutes, but because of the large number of salps collected offshore, time before preservation increased to about 10 minutes. Lengths of offshore larvae were corrected for 13 minutes of net shrinkage.

Daily increments in the otoliths were counted using a compound microscope equipped with a closed-circuit television system, a video coordinate digitizer, and a microcomputer (Methot and Kramer 1979). Age from hatching was determined from the number of daily rings in the otoliths. Because the initial ring is deposited at the time of first feeding, at about five days from hatching, time since hatching is 5 days more than the ring count (Brothers et al. 1976).

Laird-Gompertz growth curves were fit to the length at age using nonlinear regression. To compare differences in growth rates between the two sites, analysis of covariance was performed on segments of the data so that the assumption of linearity was reasonable.

Larval Production and Mortality

Age-specific larval anchovy production rates were computed from counts of larvae in 1 mm size classes to 9 mm preserved standard length (SL) from bongo tows and in 0.5 mm size classes to 7 mm SL from CalVETs. Counts of larvae were corrected for volume of water filtered, for net avoidance, and for losses owing to extrusion through the net meshes (Zweifel and Smith 1981). Larval production at each age was estimated by dividing size-specific larval abundance by time spent at each size. Duration at size was specfied from Laird-Gompertz growth curves (Methot and Hewitt 1980; Lo 1983).

Larval mortality curves were based on the Pareto decay function (Lo 1985):

$$z(t) = \beta/t$$

where $z(t)$ is the instantaneous mortality rate (IMR), β is the IMR coefficient, and t is age (days) since spawning. Daily production is given by

$$P_t = P_0(t/t_0)^{-\beta} \quad t_0 < t < 20\ d$$

where P_t is daily larval production at age t, P_0 is initial larval production (at hatching), t_0 is age at hatching, specified from hatching time as a function of incubation temperature (Lo 1983). Thus, as larvae grow older, the rate at which they appear in the next age group is diminished by the factor given by β.

The above equation (referred to subsequently as the nonlinear model) can be expressed in linear form by taking the natural logarithm of both sides:

$$\ln(P_t) = \ln(P_0) - \beta \ln(t/t_0) .$$

Both the nonlinear and the log-linear regression models can be used to estimate parameters P_0 and the IMR coefficient β. The log-linear equation is mainly used in this study to compare β between sites.

Production and mortality of anchovy larvae at Site 1 were estimated from 48 bongo samples (20 using 333 μm mesh nets and 28 using 505 μm mesh nets) and from 49 CalVETs using 150 μm mesh nets. At Site 2, these parameters were estimated from 49 bongo samples using 505 μm mesh nets and from 50 CalVETs using 150 μm mesh nets.

Larval Condition

Starvation incidence was estimated from histological criteria on 141 anchovy larvae from Site 1 and on 119 larvae from Site 2. The larvae were collected with nonquantitative bongo nets towed to 50 m. Although the best preservation procedure for histological samples is to preserve larval fish in Bouin's fixative within 3 minutes after capture, 5–6 minutes were required to obtain representative samples to 50 m. After fixing in Bouin's fluid for 24–48 hours, samples were transferred to 70% ethyl alcohol for storage.

The nutritional state of northern anchovy larvae is usually classified by grading the appearance of tissues of the brain, cartilage, notochord, liver, pancreas, and gut (O'Connell 1976). But because many of these tissues had lysed owing to extended time before preservation, an additional criterion was used in this study. This criterion, the height of midgut mucosal cells, was unaffected by the 5–6 minutes needed to fix the larvae (Theilacker and Watanabe 1989). Heights of midgut mucosal cells were divided into three categories (healthy, intermediate, and starved) according to laboratory results (Theilacker and Watanabe 1989). As northern anchovy develop past 6 mm SL, the midgut folds to increase the absorptive area. The fold makes it difficult to measure cell heights of larger larvae. To apply the durations determined for the laboratory fish to the field samples, the size of the field-collected larvae was adjusted to equal the size of preserved laboratory fish of known feeding history (Theilacker 1980). Details of these manipulations are given in Theilacker and Watanabe (1989).

RESULTS

Environmental Variations Within and Between Drifters and Sites

Surface Drift

Drifters were tracked as shown in Figure 2. Released 10 nmi apart at Site 1, Drifters A and B moved generally eastward, away from Santa Catalina Island, on slightly convergent courses. Mean speeds over their 2.7 days at sea were 17.1 cm/s and 18.7 cm/s (about 15.5 km/dy). Range of speeds measured by drifter displacements over 8 h intervals were 5.6–34.7 cm/s and 6.8–32.9 cm/s.

Released 5 nmi apart at Site 2, Drifters A and B moved in a southeast-trending arc, again on slightly convergent courses. Mean speeds over their 2.5 days at sea were 34.6 cm/s and 37.4 cm/s (about 30 km/d), twice as fast as at Site 1. Speed ranges measured were 15.3 cm/s to 45.4

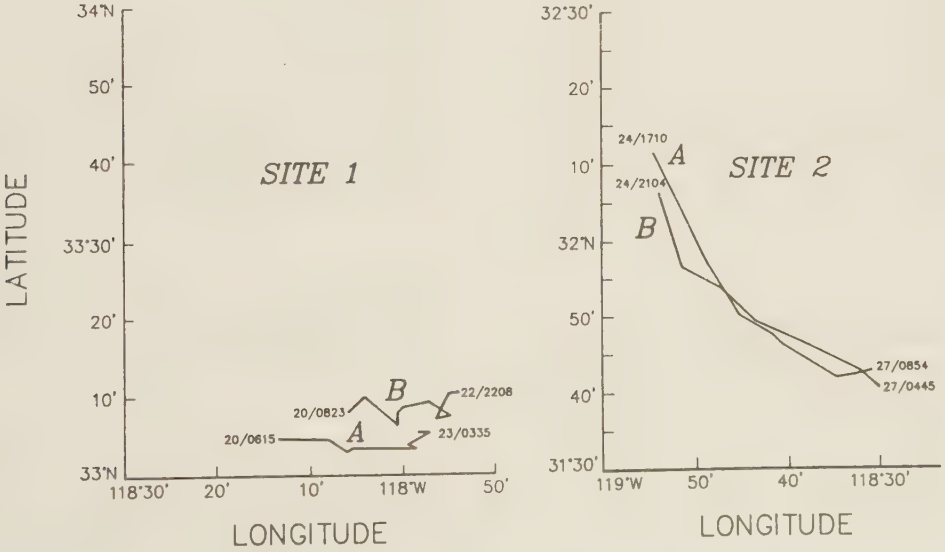
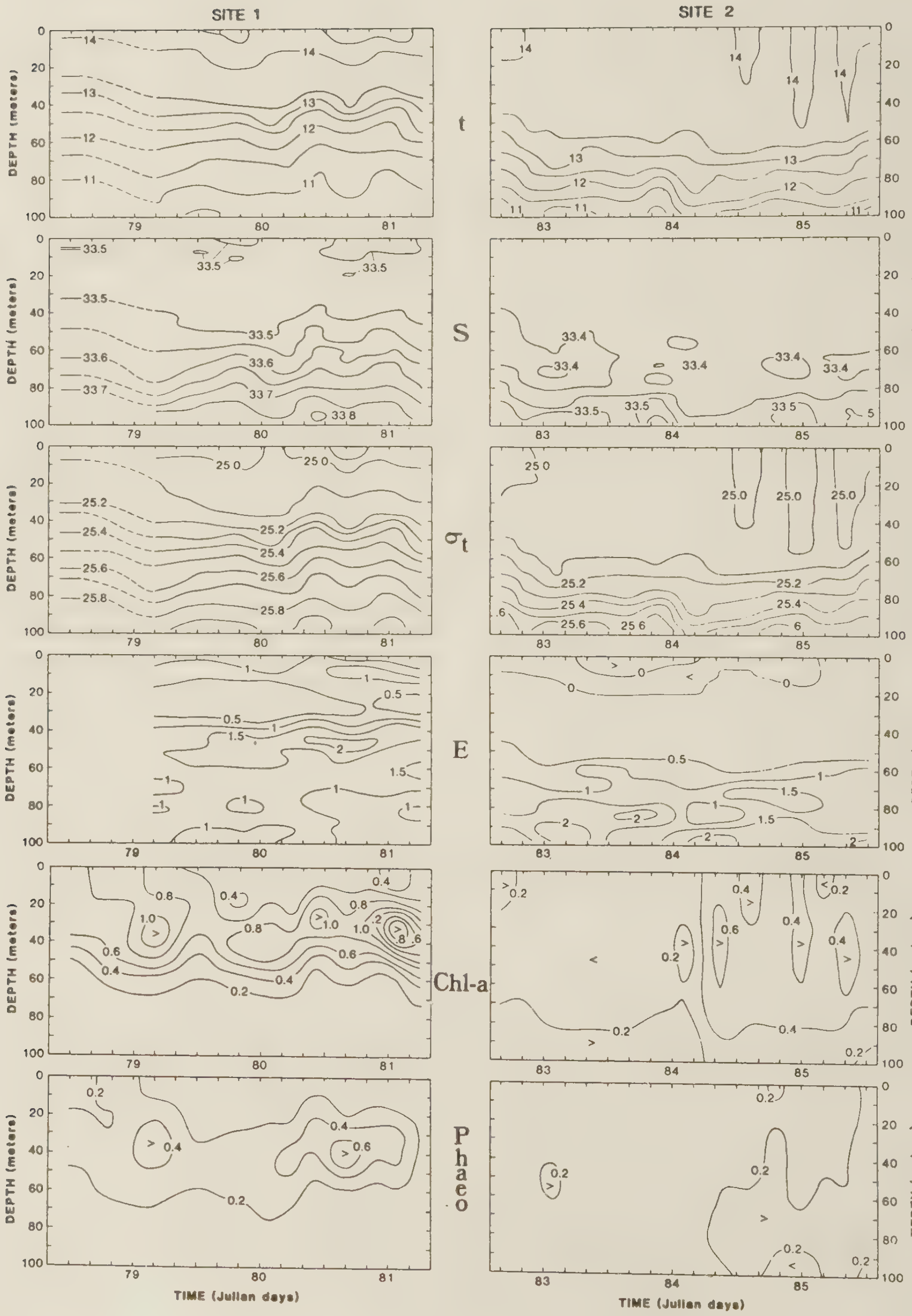


FIGURE 2.—Drifter trajectories along *Sites 1* and *2*.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σt
E
Chl-a
Phaeo
DEPTH (meters)
TIME (Julian days)
79
80
81
83
84
85
0
20
40
60
80
100
14
13
12
11
33.5
33.6
33.7
33.8
33.4
25.0
25.2
25.4
25.6
25.8
0
0.5
1
1.5
2
0.2
0.4
0.6
0.8
1.0

cm/s and 18.8 cm/s to 48.2 cm/s. Drift direction at Site 2, predominantly longshore, indicated that Site 2 larvae had been spawned offshore rather than drifting out from an onshore spawning area.

The degree to which drifter displacements paralleled one another at each site (Fig. 2) indicated homogeneous, nondivergent flow of the surface layer and general integrity of each water corpus being investigated. Similar rates of separation of drifter pairs indicated no differences between rates of lateral diffusion between sites.

Vertical Structure

Physical structure of the upper 100 m at both sites exhibited no overall trends for the duration of the study (Fig. 3). Variations of isopleth depths in the pycnocline at Site 1 were greater during the second half of the period, perhaps owing to increased internal wave activity.

A slight warming trend over the course of the studies was indicated by increased surface layer temperatures at both sites. The trend was likely due to local heating of the mixed layer. Heat content of the upper layer increased at Site 2 but no trend was detected at Site 1.

Local diurnal heating was apparent at Site 1 from continuous temperature records at 3 m depth as well as from CTD casts. Higher winds and a thicker mixed layer at Site 2 obscured diurnal temperature variations.

Vertical sections of phytopigments (Fig. 3) gives a less conservative picture of variations. Intensification of the maximum chlorophyll and phaeopigment layers over the course of studies occurred at both sites. In view of the lack of change of temperature, salinity, and density structure, the increase in pigment concentration was likely due to local processes rather than to advective processes. The change thus expressed the net product of primary production and grazing.

Composite T-S diagrams (Fig. 4), constructed from CTD cast data at each site, indicate that the drifters were set into waters of different structure and composition at the two sites. Site 2 water, closer in character to California Current core water (Lynn and Simpson in press), was cooler and less saline than Site 1 water. Site 1 water was likely derived from a mix of California Current core water (from the north, offshore) and coastal countercurrent water (from the south, nearshore), further modified by local warming of the surface layers in transit.

Plankton Quantity and Composition

Within sites, no major differences were apparent in plankton quantity or community composition along drifter paths. Over twice as many plankton organisms were caught by 333 μm mesh nets at Site 1 than at Site 2, and predatory copepods were 5 times more numerous at Site 1 than at Site 2 (Table 1). Plankton diversity was somewhat higher at Site 1 than at Site 2: on average, Site 1 tows yielded 144 invertebrate species, whereas Site 2 tows yielded 130 species. Perhaps the most striking difference in the zooplankton was the high abundance of salps at Site 2. No direct interactions are known between fish larvae and salps.

In terms both of rations and numbers, over twice as much larval anchovy food was caught by 75 μm mesh nets at Site 1 than at Site 2 (Table 1).

Summary

To compare habitats at the two sites, Table 1

FIGURE 3.—Vertical time sections of temperature (t), salinity (‰), density (σ_t), and stability (E) at Sites 1 and 2. Vertical time sections of chlorophyll-a and phaeopigment at Sites 1 and 2.

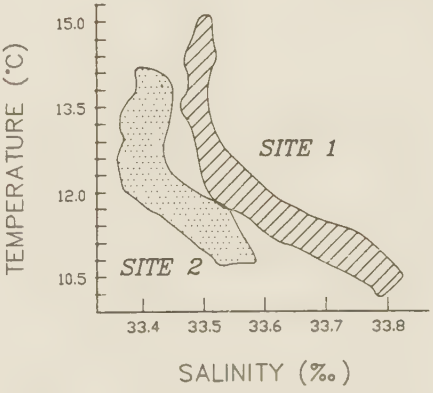

FIGURE 4.—Composite T-S diagrams at *Sites 1* and *2*.

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[3] Lynn, R. J., and J. Simpson. 1989. The influence of bathymetry upon the flow of the undercurrent off Southern California. Unpubl. manuscr.

TABLE 1.—Comparisons between study sites—means (and standard deviations) of environmental characteristics at Sites 1 and 2. *n* is number of observations. Integrations are to 50 m depth.

	Site 1		Site 2	
	mean (SD)	*n*	mean (SD)	*n*
mixed layer depth (m)	37.6 (5.0)	11	57.7 (6.8)	14
wind speed (m/s)	3.27 (1.54)	15	8.97 (2.36)	14
stability max. (E × 10^7)	4.00 (1.54)	11	3.47 (1.59)	14
depth of stability max. (m)	45.6 (7.8)	11	67.6 (8.7)	14
surface current speed (cm/s)	18.9 (10.2)	16	35.4 (10.4)	16
surface temp. (C)	14.50 (0.41)	50	14.04 (0.14)	50
surface salinity ‰	33.50 (0.011)	11	33.42 (0.044)	14
surface chlorophyll a conc. (μg/L)	0.56 (0.20)	11	0.37 (0.15)	12
surface phaeopigment conc. (μg/L)	0.14 (0.13)	11	0.10 (0.09)	12
integrated chlorophyll a conc. (mg/m^2)	45.3 (9.74)	11	33.8 (12.72)	12
integrated phaeopigment conc. (mg/m^2)	20.3 (4.77)	11	15.9 (7.64)	12
Integrated particle conc., 16–160 μm (no/cm^2)	44012 (44761)	11	66980 (67027)	5
Integrated particle conc., 50–160 μm (no/cm^2)	5854 (9405)	11	2607 (1138)	5
Secchi depth (m)	11.5 (2.0)	9	18.1 (2.7)	8
food conc. >75 μm (no/L)	31.4 (13.9)	26	13.5 (12.0)	24
food conc. >75 μm (μm^3/L)	19.6 (5.7)	26	8.1 (7.0)	24
zooplankton conc. (no/m^3)	625 (216)	26	236 (160)	24
predatory copepods (no/m^3)	121 (79)	26	24 (32)	24
zooplankton spp. (species/tow)	144	26	130	24
copepod spp. (species/tow)	65	26	60	24

gives means and variations among environmental parameters of energy input and dissipation, responses of the plankton communities, and levels of food supply and predation pressure to which the larvae were exposed. Analyses of variance of environmental characteristics demonstrated much smaller variations between drifters within sites than between sites.

In review, changes over study periods at both sites were local, not advective; we resampled the same water and larval population within sites. Vertical gradients were shoaler and more intense at Site 1. Temperature and salinity relations in the upper 100 m indicate different recent histories of the waters at the two sites. Surface layers at Site 1 were warmer, more saline, less turbulent, less transparent, and contained higher concentrations of larval foods and other plankton. Plankton community structure was different between sites: most notably, predatory copepods were more abundant at Site 1 and salps were more abundant at Site 2.

Larval Parameter Variations Within and Between Drifters and Sites

Larval Growth Rates:

Ranges of size and age of larvae differed between sites. Site 2 samples included larvae that were larger (and older) than those at Site 1. The average age of larvae was 6.9 and 11.5 days from hatching at Sites 1 and 2, respectively. Larval length averaged 7.8 mm and 9.0 mm at Sites 1 and 2, respectively. Thus the offshore Site 2 was inhabited by older and slightly longer larvae than Site 1. Offshore drift of larvae hatched inshore into the region of Site 2 (Smith 1972) may account for this phenomenon, as may higher predation on older larvae at Site 1. The latter explanation is favored because the observed flow patterns (Fig. 2) do not suggest that larvae were transported offshore from nearshore areas.

To assess the growth of larvae in these two stations, the Laird-Gompertz model was used to fit the length-age data:

$$L_t = L_\infty(L_0/L_\infty)^{\exp[-\alpha t]}$$

where t is time since first feeding at 5 days after hatching, L_0 is larval length at first feeding, and L_∞ is the asymptotic length. The maximum and minimum fish lengths in the sample have strong influence on the length parameter estimates (L_0 and L_∞) and on the growth coefficient (α). The resulting growth coefficients at the two sites (Table 2) are 0.1 for the inshore station and 0.05 for the offshore station. A standard growth coefficient of 0.05 is used by CalCOFI (Methot and Hewitt 1980).

We compared total growth rates of fish younger than 18 days (after hatching) at the two sites, assuming a linear growth rate to be reasonable because of difficulties in comparing differences between nonlinear curves. Larvae at the offshore Site 2 had a larger asymptotic length and a lower growth coefficient than at the inshore site. The null hypothesis, that growth was equal at the two sites, was tested using analysis of covariance. When the test was performed on lengths uncorrected for shrinkage or on lengths corrected for the same shrinkage, the slopes at the two sites were not significantly different but the mean lengths were. (A true difference between mean lengths would indicate that anchovy larvae had hatched at a larger size at Site 1 than at Site 2, or that Site 2 larvae underwent starvation at the first-feeding stage and then recovered.) However, when larval lengths from Site 2 were corrected for greater handling time, then neither the slopes nor the adjusted lengths differed significantly between the two sites (Table 3). In short, corrected data indicate that no difference existed in larval growth between the sites.

Larval Production and Mortality Rates

Larval production at age (larvae <20 days from spawning) was used to model larval mortality. For mortality analysis, age is defined as time since spawning. Larval production was computed as described above in Methods, and larval age was derived from live size using a Gompertz growth curve. Three growth curves were available for computing larval age: the standard growth curve used for routine annual anchovy larval assessment, and two site-specific growth curves constructed from length-age data collected at each of our sites. We elected to use the standard growth curve to convert larval size to age for both sites because no significant difference in total growth rates for larvae <20 days since spawning was detected between two site-specific growth curves, and because the growth coefficients estimated from two sites were also similar to that of the standard growth model (all equal to 0.05) when the maximum and minimum lengths of larvae were set to be 27 mm and 4.1 mm, corresponding to the standard growth curve. Both nonlinear and log-linear regression

TABLE 2.—Parameters of Laird-Gompertz growth curves for northern anchovy larvae at Site 1 and Site 2. L_0 is larval length at first feeding; L_∞ is the asymptotic length; and α is the growth coefficient. Lengths are corrected for differential handling times.

Parameter	Site 1	Site 2	CalCOFI
L_∞ (mm)	14.7 (0.6)	20.5 (1.8)	27
L_0 (mm)	4.9 (0.1)	5.2 (0.2)	4.1
α	0.10 (0.01)	0.05 (0.01)	0.05
n	234	141	—
With L_∞ (mm) fixed at 27 mm and L_0 (mm) fixed at 4.1 mm,			
α	0.05 (0.001)	0.05 (0.01)	

TABLE 3.—Comparison of growth rates of northern anchovy larvae between Site 1 and Site 2 for post-yolk-sac larvae less than 18 days old, using analysis of covariance.

Linear regression of growth. L is length, t is time since hatching, and n = total number of larvae sampled.

Site 1 $L_t = 7.33 + 0.46\ (t - 9.99)$ $n = 197$
Site 2 $L_t = 7.82 + 0.46\ (t - 11.54)$ $n = 79$

Analysis of covariance between sites

Source of variation	df	Sum of squares	Mean squares	F	Prob. (tail)
Equality of adjusted means	1	2.57	2.57	3.23	0.07
Zero slopes					
All covariates	1	709.76	709.76	892.98	0.00
error	273	216.99	0.79		
Equality of slopes all covariates and all groups	1	0.02	0.02	0.02	0.89
error	272	216.97	0.80		

were used to estimate the larval production at hatching (P_0) and mortality coefficient (β).

Mortality Estimates

Data in three arrays were used to estimate mortality: bongo larvae alone, bongo larvae plus 2.5–4.0 mm larvae from CalVETs, and bongo larvae plus 3.0–4.0 mm larvae from CalVETs (Tables 4, 5). The nonlinear regression gave estimates of β ranging from 1.15 to 2.18 (equivalent to IMR of 0.115–0.218 for larvae of age 10 days) for Site 1 and 1.06–3.03 for Site 2. The lower values of β were caused by low numbers of 2.5 mm larvae in CalVET samples. The log-linear regression produced more consistent estimates of β than those from nonlinear regression: Site 1 values ranged from 3.32 to 3.94 and Site 2 values ranged from 2.87 to 3.47. Estimates of P_0 at hatching age ranged at Site 1 from 12.03 to 28.38, and for Site 2 from 1.37 to 4.23. For all data arrays, site differences in larval production rates were apparent (Tables 4, 5), but site differences in mortality rates were not (Table 6).

Comparison of Larval Production and Mortality Coefficients Between Sites

Larval samples from bongo tows were used to compare the mortality between sites. Analysis of covariance was performed on the logarithmic transformation of age and larval production. The results of the analysis indicated that the site difference between mortality coefficients was not statistically detectable whereas site difference between larval production rates was (Table 6).

We also compared the larval production and mortality at the two sites (Table 5) with those over the northern anchovy spawning domain as sampled by the CalCOFI 8502 survey ($P_0 = 4.81$ with SE = 0.30, and $\beta = 2.21$ with SE = 0.11 for 37 positive CalVET tows out of 45). Larval production at Site 1 was much higher than the average over the CalCOFI 8502 survey region, but production at Site 2 and larval mortality at both sites were similar to the survey region averages.

Figure 5 shows the larval production-at-age curves at the two sites and, for comparison, larval production curves for anchovy spawning domains as sampled on CalCOFI Cruise 8502, just prior to our site-intensive program. Site 1 displayed high production of all larval ages, which was higher than its subdomain (CalCOFI Region 7), whereas Site 2 production was somewhat above that of its subdomain (CalCOFI Region 8) and somewhat below that of the entire spawning domain as sampled ("all regions").

Starvation Incidence

Midgut cell height is the histological criterion of larval feeding history. The range of cell height and the cell height change with larval size were similar at both sites (Fig. 6). The similarity

TABLE 4.—Northern anchovy larval production per unit area per day at age at Sites 1 and 2 from bongo and CalVET nets, based upon "regular" growth. *n* is total number of tows, pos. *n* is number of tows with larvae.

	Site 1		Site 2	
Capture size (mm)	Average age (d)	Production no./0.05 m²/d	Average age (d)	Production no./0.05 m²/d
Bongo net				
2.5	4.72	10.67	5.29	0.95
3.75	8.30	5.57	9.20	0.19
4.75	11.04	0.54	11.91	0.074
5.75	13.44	0.16	14.38	0.033
6.75	15.64	0.096	16.69	0.024
7.75	17.78	0.085	18.86	0.022
8.75	19.84	0.095	21.06	0.016
n(pos.*n*)	48 (48)		49 (46)	
CalVET net				
2.5	3.60	6.44	3.81	0.674
3.0	5.09	7.81	5.37	1.221
3.5	7.16	7.65	7.56	1.503
4.0	8.90	3.19	9.27	0.445
4.5	10.10	0.27	10.50	0.098
5.0	11.41	0.44	—	—
5.5	12.86	0.04	—	—
6.0	13.38	0.04	—	—
6.5	14.78	0.02	—	—
n(pos.*n*)	49(49)		50(40)	
temperature	14.25C		14.05C	
hatching age	3.05d		3.23d	

[1] Production computed from total number of tows(n).

TABLE 5.—Estimated northern anchovy larval production at hatching (P_0) and mortality coefficient (β) from nonlinear and log-linear regression for Sites 1 and 2 using various data sets and "regular" growth parameter estimates.

	Site 1			Site 2		
Data sets	P_0 (SE)	β (SE)	MSE	P_0 (SE)	β (SE)	MSE
Nonlinear						
bongo only	28.38 (7.70)	2.18 (0.47)	1.78	4.23 (0.15)	3.03 (0.07)	0.0008
CalVET (2.5–4.0 mm) and bongo	12.03 (2.98)	1.15 (0.38)	6.01	1.37 (0.51)	1.06 (0.52)	0.1816
CalVET (3.0–4.0 mm) and bongo	23.79 (5.86)	1.85 (0.38)	2.47	2.99 (1.40)	1.80 (0.68)	0.1238
Log-linear						
bongo only	4.49 (0.77)	3.9 (0.54)	0.43	1.41 (0.22)	3.05 (0.15)	0.03
CalVET (2.5–4.0 mm) and bongo	3.79 (0.59)	3.32 (0.48)	0.74	1.36 (0.52)	2.87 (0.42)	0.57
CalVET (3.0–4.0 mm) and bongo	4.67 (0.58)	3.94 (0.45)	0.46	2.22 (0.49)	3.47 (0.38)	0.31

suggests that both larval populations had experienced comparable feeding conditions.

Although average daily mortality rates due to starvation of first-feeding anchovy larvae were higher at Site 1, 24%/d, than at Site 2, 12%/d (Table 7), the difference between sites was not statistically significant ($\chi^2 = 2.26$; $P > 0.15$). Incidence of starvation was low or nil after the first-feeding stage at both sites.

TABLE 6.—Comparison of mortality coefficients (β) of northern anchovy larvae (<20 days) between Site 1 and Site 2, using analysis of covariance. P_t is the larval production at age t; t is age (d) from fertilization. The values 3.05 and 3.23 are ages at hatching.

Log-linear regressions of mortality are

Site 1 $\ln(P_t) = 4.49 - 3.90\,[(\ln(t/3.05))]$

Site 2 $\ln(P_t) = 1.4 - 3.05\,[(\ln(t/3.23))]$

Analysis of covariance between sites

Source of variation	df	Sum of squares	Mean square	F	Prob. (tail)
Equality of adjusted means	1	13.26	13.26	50.90	0.00
Zero slopes					
All covariates	1	35.12	35.12	134.80	0.00
error	11	2.87	0.26		
Equality of slopes all covariates and all groups	1	0.52	0.52	2.24	0.17
error	10	2.34	0.23		

DISCUSSION

We had expected to find higher rates of larval northern anchovy growth and survival in the inshore than in the offshore environment. Bias or low precision cannot explain the similarity of growth and mortality coefficients between sites. The larval anchovy parameters might have been biased had we sampled larval populations imported from other sources by advection or diffusion over the course of the measurement periods, but our time series of environmental characteristics display no shifts to indicate short-term change of properties or of populations at the drifters. Similarly, lack of precision cannot be invoked: the number of tows and larvae were sufficient to distinguish mortality coefficients (β) differing by 0.5 with an 86% probability (Lo et al. 1989). We must accept that the mortality coefficients were and that many more similar tows would be necessary to distinguish between them.

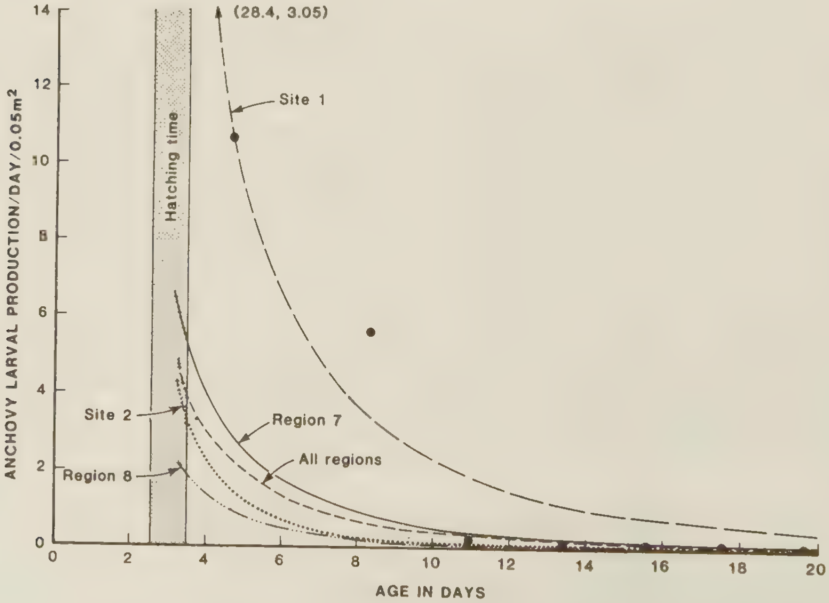

FIGURE 5.—Daily larval production vs. age for northern anchovy and fitted larval mortality curves for Site 1 and Site 2, and for CalCOFI 8502 survey and subregions. Points are for Site 1 only.

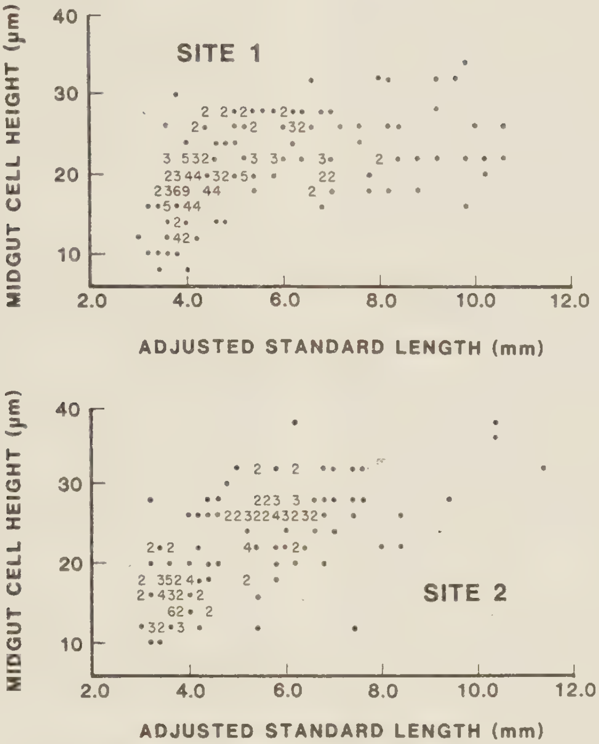

FIGURE 6.—Midgut cell heights of individual northern anchovy larvae collected at Site 1 (inshore) and at Site 2 (offshore).

TABLE 7.—Histological condition of larval northern anchovy at Sites 1 and 2. *n* = number examined; dur = duration; *n*/d = number/day; S = starved; I = intermediate; H = healthy; %/d = % dying/day due to starvation.

	Site 1					Site 2				
	S	I	H	total	%/d	S	I	H	total	%/d
3–4 mm (SL)										
n	9	17	28	54		4	32	21	57	5
dur	2	5	2.5			2	5	2.5		
n/d	4.5	3.4	11.2	19.1	24	2.0	6.4	8.4	16.8	12
4–5 mm (SL)										
n	1	11	48	60		0	5	20	25	
dur	2	3	2.5			3	3	2.5		
n/d	0.3	3.6	19.2	23.1	1	0	1.7	8	9.7	0
5–6 mm (SL)										
n	0	0	27	27	0	0	2	35	37	0
Total number examined				141					119	

Similarity of growth and starvation indices at the two sites indicates that most larvae had encountered sufficient forage to sustain "normal" growth rates, or that the fraction that had not done so were quickly removed from the system, i.e., not represented in our collections. Food abundance estimated from integrative tows may not reflect the actual availability of food to larvae because microplankton prey frequently occur in patches and laminae of very small extent (cf. Owen 1989). Also, larvae may have been sustained on food that passed through the net. Fewer larvae were collected at Site 2 than at Site 1, but starvation incidence was at least as low there as at Site 1. Furthermore, Site 2 larvae were growing as fast as those at Site 1, even though average microplankton concentration at Site 2 was less than half that at Site 1. Despite lower average food concentrations, there were zones at Site 2 that evidently contained enough food to support growth of the larvae.

An analogous result is given by Butler (1989), which showed that periods of diminished forage production, such as el Niño, have no discernible effect on growth rates of field-caught larvae. But Theilacker and Watanabe (1989) showed by experiment that starvation measurably retards larval growth. This apparent paradox is resolved if, in the sea, larvae that survive to be sampled have found enough food to grow at normal rates even in abnormal periods, whereas larvae that have been deprived to the extent that their growth is adversely affected soon vanish, perhaps by predation owing to their weakened condition rather than by starvation directly.

In contrast with the common view that northern anchovies broadcast sex products indiscriminately with the strategy that some get lucky, we advance the hypotheses that anchovy spawn where their offspring are equally likely to survive, even under widely different environmental conditions, and that these conditions mediate their spawning intensity. This is the central theme of MacCall's (1983) "Basin Model" of habitat selection by the northern anchovy.

The Basin Model postulates that when a population is large, its adults occupy less suitable habitats in which mortality of spawn per capita tends to equal that in more favorable habitats. This occurs because cannibalism of spawn by adults is higher in favored habitats than in peripheral habitats.

We roughly partition sources of overall larval mortality (β_t) into that due to cannibalism (β_c) and that due to other causes (other predation, β_p, and starvation, β_s). Diffusive change, a source of "apparent" mortality, is assumed from physical arguments above to be the same at both sites. Thus,

$$\beta_t = \beta_c + \beta_p + \beta_s \; .$$

If higher egg concentration denotes higher adult occupation, β_c was greater at Site 1 than at Site 2. Anchovy egg concentration at Site 1 averaged $37/m^3$, 15 times the egg concentration at Site 2. This difference is too great to be attributed to differences in batch fecundity of the spawners, which varies by a factor of about two (Hunter et al. 1985).

For larval mortality, β_t, to have been equivalent at the two sites, mortality from other sources ($\beta_p + \beta_s$) is required to have been greater at Site 2 than at Site 1 to the degree of offsetting the difference between sites in parental consumption of spawn (β_c). But neither larval growth rates nor starvation incidence differed between sites, showing that their β_s values were about equal. This being so, cannibalism was offset by other predation rather than by starvation. This requires increased predation (β_p) at Site 2 over that at Site 1.

For comparison of β_p between sites, we formed rough indices of predation pressure, P, from catches by vertical net tow pairs. P is the concentration of the five most numerous predators caught by the 333 μm mesh net, divided by concentration of anchovy eggs and larvae caught in the corresponding 150 μm mesh net. Predator populations in the samples consisted mainly of raptorial copepods and chaetognaths. Mean values of P were 2.8 predators/anchovy at Site 1 (26 tows) and 5.5 predators/anchovy at Site 2 (24 tows). This difference indicates compensatory predation at Site 2. Confirmation of compensatory predation, however, is not possible from this data set because our nets missed larger, faster predators such as euphausiids, and because species-specific and size-specific predation rates are largely unknown.

CONCLUSIONS

Among the several characteristics of the ichthyoplankton investigated at contrasting habitat sites, only one, larval production rate, was clearly different between sites. Growth and mortality rates were statistically indistinguishable between sites. Mortality due to starvation was about the same at the two sites. Larval production at Site 1 was well above the CalCOFI survey average, but Site 2 production and larval mortality at both sites were similar to those over the entire CalCOFI region.

Habitat characteristics at the two sites differed substantially. Site 1 was relatively eutrophic, as seen by its high concentrations of larval forage, zooplankton, chlorophyll, and phaeopigment. Site 2 was much more energetic, as seen by its greater wind speed, current speed, mixed layer depth, and depth of maximum stability. With the exception of predatory copepod abundance, every measured characteristic of the environment favored larval anchovy well-being more at Site 1 than at Site 2.

Yet the well-being of anchovy larvae was about the same at the two sites. Anchovies spawned under conditions where their larvae could grow and survive at about the same rates, despite the differences noted in the respective environments. Similar larval growth rates and the low incidence of starving larvae indicate adequate forage availability in both habitats. In agreement with MacCall's (1983) Basin Model, rates of larval anchovy mortality at the two sites were not greatly different and the same fraction of the original larval production survived to the schooling stage.

We consider this work to be a pilot effort to stimulate and guide research that we hope will be more experimental in scope and execution. To test our hypotheses, environments that more completely span the "suitable basin" need to be described and occupied long enough to follow characteristics of larval fish cohorts from egg to metamorphosis.

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Identification of Habitat of Juvenile Snappers in Hawaii

Deepwater snappers have high commercial and recreational value throughout the tropics, and their fisheries and species biology have been widely studied. However, little is known about the ecology of the juveniles between settlement to the demersal habitat and recruitment to the adult population (Munro 1987). In Hawaii, no information regarding location, size, or habitat of juvenile lutjanids has emerged after more than a decade of concentrated studies of adult stocks (Ralston 1980; Humphreys 1986). The absence of observations and collections of juvenile lutjanids or of their occurrence as prey items in the adult habitat suggests that they settle elsewhere prior to recruitment.

Adult snappers have been frequently reported as being associated with structural relief at depths of 100–500 m (Parrish 1987). In contrast, juveniles have not been caught or visually observed in such habitats in surveys made with scuba or submersible vehicles (Ralston et al. 1986; Moffitt et al. 1989). Owing to the lack of conventional scientific evidence about the habitat of juveniles, occasional reports of juveniles captured by shallow-water recreational fishermen in Hawaii continued to go largely unnoticed by researchers until one angler brought back live juvenile specimens of both *Pristipomoides filamentosus* and *Aprion virescens* in September 1988. This tangible evidence provided the stimulus to conduct some exploratory fishing in relatively shallow waters and to attempt to visually observe the fishes' habitat. This report summarizes the results of that investigation.

Methods

During October 1988, the bottom was fished and observed with scuba at three stations off the eastern side of the Hawaiian Island of Oahu. Stations 1 and 2, separated by 2 km along the coast, were situated outside the barrier reef and between the two main entrance channels of Kaneohe Bay; station 3 was located southeast of Mokapu Peninsula in Kailua Bay (Fig. 1). Most fishing was done in midmorning (0800–1200). At station 3, one afternoon and evening sampling was taken in addition to the morning sampling.

A single day of intensive fishing was done at each station from a small boat with two lines, each bearing three No. 10 circle hooks baited with live shrimp. Fishing was limited to depths of 31–76 m, to allow observation of habitat by scuba. At each station, the boat drifted or occupied sequential, anchored positions along a transect across the bottom contours while the fishing lines were bounced off the bottom. The depth was measured periodically during fishing and immediately following the landing of juvenile bottom fishes.

Habitat observations with scuba were performed at the three stations on mornings soon after the sampling was completed, at the locations and depths where target species had been caught earlier. Fishing with a single line helped confirm observation locations on two occasions: target species were landed immediately before or during the dive. At least two dives were made at each station, one or more in shallow (40–50 m) and the other in deep (51–76 m) water. At stations yielding no fish in either depth range, observations were conducted at depths similar to those yielding fish at the other stations. With the exception of the 52 m dive at station 2, dives in the deep ends of the transects occurred at what proved to be the most productive fishing depths (>61 m). Restricted bottom time at these depths limited diving activities to observing habitat and scanning an area of about 6,000 m^2 for target species.

Additional specimens were concurrently collected from waters off Lahilahi Point on western Oahu by the same methods, except that artificial bait was used on a single line and depth was only estimated (60–90 m) by the amount of line deployed. Stomachs and hindguts of *P. filamentosus* from all sources were examined, and prey items were counted and roughly classified. The *P. filamentosus* containing food items were used in the analysis of occurrence (prey type as a percentage of all individuals eaten) and frequency (percentage of fish containing each prey type).

Results and Discussion

A total of 36 juvenile lutjanids were collected from the three stations (Table 1). *Pristipomoides filamentosus* (n = 30) were caught at all three stations, all at 61–73 m depths; 25 were captured at station 1. Five *Aprion virescens* and the one *Aphareus rutilans* were taken at station 2 at 40 m. At stations 1 and 2, the catch rate consistently declined at all depths in the late morning hours. At station 3, no fish were caught until dusk, when four *P. filamentosus* were

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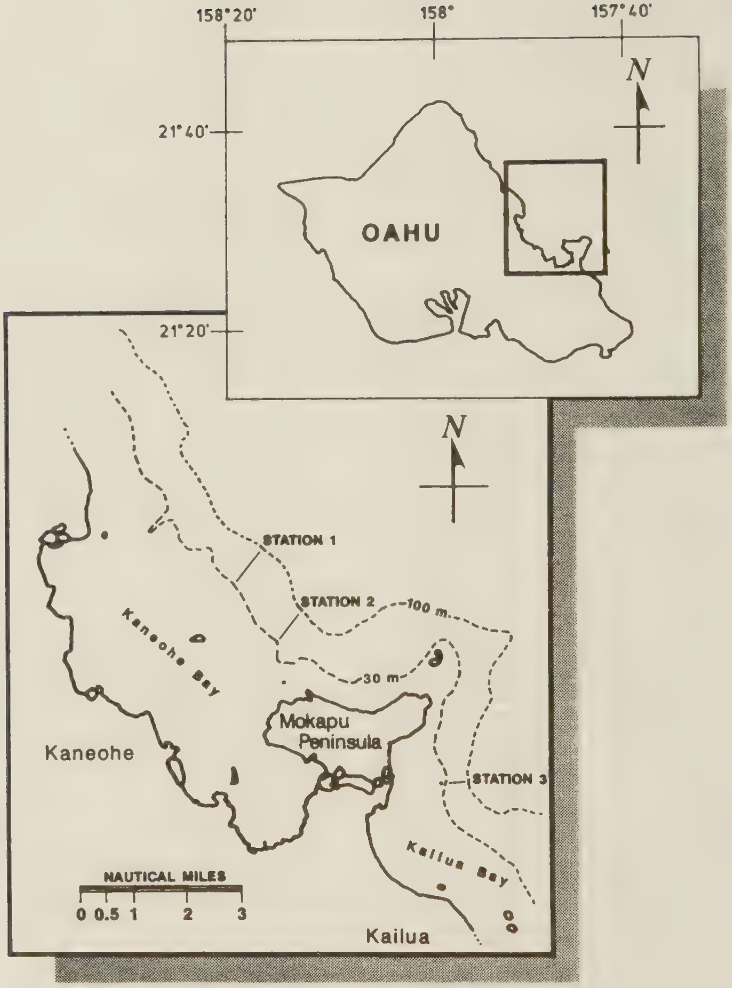

FIGURE 1.—Locations of the three established east Oahu stations.

taken. The west Oahu site yielded seven more *P. filamentosus* for analysis. These results suggest a possible minimum depth of about 61 m for juvenile *P. filamentosus* at the sampled sites.

The scuba observations indicated that the habitat was generally similar at all three stations, but the substrate within each station varied with depth. At the shallow end, the bottom was hard, flat, and devoid of vertical relief. A thin veneer of sand was present, with stands of live *Halimeda* algae evenly distributed over the bottom. Infrequent, shallow depressions in the bottom provided the only substantial relief in which newly settled reef fish (e.g., Pomacentridae and Labridae) were aggregated. No juvenile lutjanids were sighted at this shallow habitat at any of the three stations, although during observation of the habitat at station 2, two *Aprion virescens* were hooked.

The bottom habitats observed at the deep ends of stations 1 and 3, where nearly all the *Pristipomoides filamentosus* were caught, were also similar. The bottom was flat and almost completely devoid of any relief other than minor features produced by sparse benthic biota. The substrate consisted entirely of soft, deep sediment heavily penetrated by burrowing invertebrates. Although no fish were seen during these deep dives, their presence was established at station 1 by the capture of a single *P. filamen-*

TABLE 1.—Results from sampling at three stations on the eastern side of Oahu and at a supplementary site off west Oahu. Numbers in parentheses indicate the actual dive depths (in meters).

Species caught	Depth (m)	Bottom substrate by depth range	
		40–50 m	51–76 m
Station 1			
25 *Pristipomoides filamentosus*	61–73	Hard, flat, with *Halimeda* algae (43)	Flat, soft, fine sediment with invertebrate burrows (69)
Station 2			
5 *Aprion virescens*	40	Hard, flat, with *Halimeda* algae (40)	Flat, coarse sand, without fine sediment (52)
1 *Aphareus rutilans*	40		
1 *P. filamentosus*	67		
Station 3			
4 *P. filamentosus*	67	Hard, flat, without *Halimeda* algae (43)	Flat, soft, fine sediment with invertebrate burrows (70)
West Oahu			
7 *P. filamentosus*	>61		
1 *Aprion virescens*	>61		

tosus at anchor just prior to the dive. At station 2, a somewhat shallower (52 m) dive revealed a substrate consisting entirely of soft *Halimeda* sand without invertebrate burrows or visible fine sediment. After the bottom observations, additional fishing at >61 m depths yielded a single *P. filamentosus*.

Since the density of juvenile lutjanids was probably not great at any location, it is not surprising that they were never sighted by divers. Avoidance behavior by the juveniles may have contributed to the lack of sightings. Our impressions of the habitat based on dive observations were consistent with those from other surveys of the study area (Smith et al. 1973; Coulbourn et al. 1988).

The portion of the life cycle during which juveniles occupy the observed habitat remains unknown. Fork lengths (FL's) of the collected *P. filamentosus* (n = 32) ranged from 10.1 to 20.7 cm; most individuals were clumped at the low end of the range. Planktonic individuals as large as 5 cm have been recorded for a somewhat smaller species, *P. sieboldii*, by Leis (1987). Until the present study, the smallest recorded *P. filamentosus* was 18 cm FL, caught by handline during sampling for adults (Ralston 1981). Using Ralston and Miyamoto's (1983) estimated growth curve derived from adult specimens, a fish of 18 cm FL would be approximately 1 yr old.

Larger identifiable prey items recovered from the stomachs of 22 juvenile specimens of *P. filamentosus* included early juvenile fish (probably recently settled) and cephalopods (including an octopod) (Table 2). The hindgut contained small planktonic crustaceans, appendicularians, and other gelatinous plankton. Most prey individuals were small, but the general taxonomic composition of the diet of the juveniles did not appear greatly different from that of adults. Crustaceans and salps commonly occur in the diet of adult *P. filamentosus* (Kami 1973; Parrish 1987).

TABLE 2.—Approximate percentage of number and frequency of identifiable prey items found in *Pristipomoides filamentosus* juveniles (n = 22).

Prey type	Percent occurrence	Percent frequency
Juvenile fish	2	18
Fish scale	3	18
Small crustaceans	90	72
Cephalopods	2	9
Gelatinous plankton	3	18

Relatively flat, soft bottoms such as occur at these stations have been largely ignored as potentially important habitat for these deepwater lutjanids, but they may provide essential habitat for the juveniles. Artificial structures placed in depths of 61–117 m in Hawaii successfully aggregated deepwater lutjanid adults, but failed completely to attract juveniles (Moffitt et al. 1989). Although there is little evidence that juveniles avoid such high relief features, there is no evidence of positive association. The limited gut samples from our juveniles did not indicate any material endemic to hard substrate (e.g., coral; obligate, hard bottom-associated invertebrates). Association with structural relief or even with adult bottom fish may put juveniles at risk (Johannes 1978). For example, predators may routinely visit high structural features. Thus, juveniles may pass their early settled life on flat, soft, featureless bottoms. The use of special habitats by prerecruits to avoid competition and possible predation has been observed in both temperate (Carlson and Haight 1976) and tropical fishes (Shapiro 1987). Juvenile lutjanids may also occur on hard, flat bottoms with some limited degree of relief. No fishing on such bottoms was attempted, and extensive sampling effort would be required to eliminate the possibility that such habitat is used.

This brief, preliminary investigation has demonstrated only the presence of juveniles of recreationally and commercially important lutjanids in habitat relatively close to the fishing grounds for adults, but not where adults congregate. The boundaries of that habitat and the characteristics that make it attractive to juveniles remain to be defined. Some basic attributes, such as depth, temperature, substrate, and the general nature of bottom relief, are relatively easy to measure and describe for large areas. Characterization of the habitats used by juvenile lutjanids will improve the ability to assess and manage productive substrate. Ichthyoplankton sampling has yielded relatively few specimens of larval lutjanids (Collins et al. 1980; Leis 1987), and the value of that approach for assessing adult stocks seems limited. A focused program of sampling and monitoring the juvenile population and estimating the available habitat suitable for them may provide more effective indicators of potential recruitment and indicate the prospects for future adult stocks.

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REVIEW/SYNTHÈSE

The Monotypic Sardines, *Sardina* and *Sardinops*: Their Taxonomy, Distribution, Stock Structure, and Zoogeography

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This paper reviews the taxonomy, distribution, stock structure, biochemical genetics and zoogeography of the world's two subtropical sardines, *Sardina* and *Sardinops*. We conclude that both genera are monotypic and that the differences between populations of *Sardinops* in different current systems are not large enough to consider them distinct subspecies. Analysis of biochemical genetics information, fossil evidence, and present and paleoclimatic conditions suggests that *Sardinops* did not achieve its present distribution until the Pleistocene and that westward exchange of sardines via the northern and southern west wind drift regions is possible with present climatic conditions. Transequator exchange appears to be possible only during glacial maxima and only in the eastern tropical Pacific.

Notre étude fait le point sur la taxinomie, la répartition, la structure des stocks, la génétique au niveau biochimique et la zoogéographie des deux sardines subtropicales du monde, *Sardina* et *Sardinops*. Nous en concluons que les deux genres sont monotypiques et que les différences entre les populations de *Sardinops* dans les divers systèmes de courants ne justifient pas leur séparation en sous-espèces distinctes. L'analyse des données génétiques, des éléments fournis par les fossiles et des conditions présentes et paléo-climatiques semble indiquer que *Sardinops* n'a réalisé sa présente répartition qu'au pléistocène et que l'échange de sardines vers l'ouest via les régions nord et sud de dérive due aux vents d'ouest est possible dans les conditions climatiques actuelles. L'échange à l'équateur ne semble possible que pendant les maxima glaciaires et dans l'est du Pacifique tropical.

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A small assemblage of species dominates the subtropical fish faunas of the world's eastern boundary currents (Bakun and Parrish 1980). The assemblage includes four types of small pelagic fishes; sardine (*Sardina* and *Sardinops*), anchovy (*Engraulis*), mackerel (*Scomber*), and jack mackerel (*Trachurus*). The same assemblage also dominates the epipelagic fish faunas of the subtropical portions of most of the western boundary currents. The most significant exception to this is the Gulf Stream region where sardines (*Sardina* or *Sardinops*) are absent and *Engraulis*, while abundant, is not a dominant species. The Brazil Current–Falkland (Malvinas) Current region also lacks *Sardina* or *Sardinops*, but the other types dominate the subtropical, epipelagic fish fauna in this region.

The four types account for about 30% of the world's catch of marine fishes. For most of the last 25 years either *Sardinops* or *Engraulis* has supported the world's largest fisheries and *Sardinops* is presently the largest single component of the world's harvest of fishes.

There has been a long history of economic and scientific interaction between the major fisheries on this assemblage of fishes, both within geographical areas and among areas. Fishing vessels catching one of these fishes usually also catch the others. The world's trade in fish meal is dominated by these fishes and they comprise a large proportion of the world's canned fish. Information, technology and material used in the fisheries for these fishes has been transferred from one area of the world to another for many decades. For example, the development of the California pelagic fishery was heavily influenced by canning technology developed for sardines in Europe (Thompson 1921) and the round-haul nets used in the early

California fishery were originally developed in Rhode Island, Italy, and Japan (Higgins and Holmes 1921; Scofield 1924). Much of the modern purse seine technology (Fry 1931), large-scale fish meal plants (Scofield 1921), and the first factory reduction ships (Scofield 1938) were developed in California. When the California sardine population collapsed much of the technology, and in many cases canning and fish meal machinery were transferred to South Africa, Peru, and Chile which fostered further development of both harvesting and processing technology. During the recent development of the Chilean sardine and jack mackerel fishery there were significant technological and investment transfers from South Africa. In Europe and Japan, where there were longer traditions of marine fisheries and local markets, development has had less interaction with other regions.

Transfer of research methodology and results between the research establishments in the various regions has also been extensive and continuous. However, whereas the transfer of methodology has been acccomplished very rapidly it is unclear whether the results from research in one area can be transferred to another area. One of the reasons for this is that there is an understandable tendency to assume that widely dispersed populations of admittedly very similar fishes (for example the various *Sardinops* populations) might be expected to have evolved adaptations which would be specific to their individual habitats. This assumption has been reinforced by the continued use of different species names in different regions.

With few exceptions, early taxonomists described a different species of sardine, mackerel, anchovy, and jack mackerel for each current system; in many cases they were originally described as different genera. Within each of the four groups of fishes the recent trend of taxonomy has been towards a reduction in the number of species. As will be shown later, in *Sardinops* there is a long history of publications documenting the fact that the "species" in different regions have no demonstrable differences. However, local scientific names continue to be used in most regions. In *Scomber* it is evident that there are only three species; *S. japonicus* which occurs in all of the major eastern and western boundary currents, *S. australasicus* which occurs in the Indo-Pacific (Kijima et al. 1986), and the temperate form *S. scombrus* which is found only in the North Atlantic (Collett and Nauen 1983). In *Engraulis* a separate species has been considered to occur in each current system and Nelson (1984) has suggested a separate subgenus for the forms in the California, Peru, and Falkland (Malvinas) currents. Also several taxonomic studies in progress suggest that *Engraulis* may be divided into two or three genera. In *Trachurus* the present taxonomic situation can only be described as confused, with papers that describe new species overlapping those that synonymize forms from widely dispersed areas of the world (Nekrasov 1978; Rytov and Razumovskaya 1984; Parrish 1989).

The question as to whether geographically isolated populations are distinct at the genus, species, subspecies, race, or fisheries stock level has significance far beyond the narrow range of taxonomy. If the distinctions among populations in widely separated current systems tend to be well below the species level, it is implied either that individual current systems are not closed systems for the species and that some exchange between current systems occurs or that the species has only recently (on a geological time scale) achieved its present geographical distribution. This would have great implications for research programs as diverse as evolutionary theory, zoogeography, ecosystem analysis, and fisheries management. In addition it would greatly enhance the value of interregional comparative analyses (Parrish et al. 1983).

In this work we have attempted to present the available taxonomic, genetic, geographical distribution, and stock structure information for one of these dominant and widespread ecotypes, the subtropical sardine, and to use this information to examine the degree of interchange which occurs among and within subtropical neritic regions of the world ocean.

Taxonomy

The Clupeidae are a difficult group to deal with taxonomically. Scores of genera and over 300 species have been described. A large proportion of these taxa has proved to be invalid and the status of other taxa is presently unresolved. One of the difficulties is that similar forms occurring in widely separated, but ecologically similar, regions of the world were originally described as separate species or even genera. As mentioned previously, local biologists continue to use old scientific names for many of these forms even after they have been shown to be indistinguishable from the forms in other regions. The sardines, or pilchards, are a good example of the present situation.

The North Atlantic–Mediterranean sardine, *Sardina pilchardus* (Walbaum 1792) was the first sardine to be described. It was originally described as *Clupea*, as were most of the *Sardinops* ecotypes described from 1842 to 1879. Valenciennes (1847) created the genus *Sardinella* to describe a tropical species of sardine, and for a few years some of the subtropical sardines were also referred to as *Sardinella*.

Gunther (1868) included all of the Clupeidae having a terminal mouth, minute or absent teeth, a complete midventral series of scutes, and an anal fin in the genus *Clupea*. Thus the subtropical sardines were included in the genus *Clupea* by most workers. Regan (1916, 1917), in his revisions of the Clupeidae, separated the sardines into a subtropical genus *Sardina* and a tropical genus *Sardinella*. Regan also examined sardines from all of the major subtropical areas of the world and decided that there were three species of *Sardina*:

1) *Sardina pilchardus*. With two subspecies; *S. p. pilchardus* off the Atlantic coast of Europe, from Portugal northwards to the British Isles, and *S. p. sardina* in the Mediterranean and off the Atlantic coast of North Africa.
2) *Sardina sagax*. With four widely separated populations; off the Pacific coast of South America, off the Pacific coast of North America, off Japan, and off South Africa.
3) *Sardina neopilchardus*. With populations off Australia and New Zealand and which Regan suggested was closely related to *S. sagax*.

Svetovidov (1952) in his extensive work on the Clupeidae repeatedly pointed out the close relationships between the "Clupeinea which migrate extensively and live mainly in the upper layers of the water (*Sardinops*, *Sardina*, *Sardinella*)." He notes the following unique characteristics which they share:

1) The dorsal fin is closer to the front of the body in *Sardina*, *Sardinops*, and *Sardinella*.
2) The lateral line canals on the head are most devloped in *Sardina*, *Sardinops*, and *Sardinella*.
3) The last two fin rays of the anal fin are elongated into lobes in *Sardina*, *Sardinops*, *Sardinella*, and *Clupeonella*.

4) Individuals have dark lateral pigment spots on the body in *Sardina*, *Sardinops* and some species of *Sardinella* and *Harengula*.
5) There are two elongated scales on the base of the lobes of the caudal fin in *Sardina*, *Sardinops*, and *Sardinella*.
6) There are transverse striations on the body scales which are interrupted in the center in *Sardina*, *Sardinops*, and *Sardinella* and unbroken in *Harengula*.
7) There are radial striations on the operculum of *Sardina* and *Sardinops*.

The major characteristics which separate the three genera are:

1) In *Sardina* the body scales are variable in size with smaller scales hidden underneath the larger scales.
2) In *Sardinops* the gill rakers on the lower part of the gill arch decrease in size toward the corner of the arch and the rakers on the upper part of the arch overlap the rakers on the lower part.
3) In *Sardinella* there are bilobed dermal outgrowths on the vertical portion of the cleithrum and there are no striations on the operculum.

Thompson (1926) in a morphological comparison of the European sardine (*S. p. pilchardus*) and the California sardine, which he called *Sardina sagax*, described a number of characteristics which could be used to separate the species. Hubbs (1929) used Thompson's results to establish a new genus, *Sardinops*, in which he included Regan's *Sardina sagax* and *Sardina neopilchardus*. His new genus was based on the six characteristics listed below:

1) In the American species there is usually a row of dark blotches behind the head, typically not apparent in the European.
2) The scales in the American species are arranged in a regular order, whereas the European are irregular with each alternating row not being nearly overlapped by the one in front.
3) The ventral scutes are weaker and less keeled, and have less expanded bases than the European species.
4) The gillrakers on the lower limb, unlike the European species, are shortened at the angle of the arch and they differ markedly in number at comparable sizes. In addition the upper limb folds down over the lower limb near the angle and there are differences in the minute processes on the gill rakers.
5) The interopercle is more expanded and widely exposed behind the preopercle.
6) The opercular ridges (and preopercle edge) are strongly oblique instead of being nearly vertical.

Hubbs (1929) examined *Sardinops* from California, Chile, Japan, and Australia and although he found no differences between these forms and even mentioned that "The distinctness of *Sardinops caerulea* is particularly doubtful," he differed from Regan (1916) and Thompson (1926), and used different scientific names for the populations in each of the major current systems in which the form occurs. Therefore the accepted usage for *Sardinops* became as follows:

1) *Sardinops sagax* (Jenyns, 1842)	Chilean
2) *Sardinops melanosticta* (Temminck & Schlegel, 1846)	Japanese
3) *Sardinops ocellata* (Pappe, 1853)	South African
4) *Sardinops caerulea* (Girard, 1854)	Californian
5) *Sardinops neopilchardus* (Steindachner, 1879)	Australian

A number of taxonomic studies have been carried out comparing various populations of *Sardinops*. Thompson (1926) found no significant differences in sardines from California, Japan, and Peru. Taranets (1938) was unable to find significant differences between the Japanese and California sardines and suggested that the two forms were subspecies. He also found that Japanese and California sardines had keel scales that were essentially the same as those in *Sardina*, thus invalidating one of the characteristics Hubbs (1929) used to create the genus *Sardinops*. Fowler (1941) agreed with Regan (1916) in including the South American, Californian, South African, and Japanese forms as a single species; however, he considered the use of the genus *Sardina* invalid and suggested that the proper name for all of the subtropical sardines was *Arengus*. The usage of the generic name *Arengus* was, however, not picked up by most authors. Amemiya and Tamura (1943) concluded that the degree of difference between the Japanese and California sardines was no more than typically occurs within a single species. Hildebrand (1946) examined *Sardinops* from Peru and California and found differences which he considered significant only at the subspecies level.

Svetovidov (1952) considered all of the populations of *Sardinops* to be the same species, *Sardinops sagax*. He also stated that *Sardina* often has lateral pigment spots and pointed out that this is a characteristic which it shares with *Sardinops* and *Sardinella*. This invalidated another characteristic which Hubbs (1929) used to establish the genus *Sardinops*.

De Buen (1958) examined sardines from Chile, Peru, and California and used the results of Thompson (1926) and Hildebrand (1946) to propose that there were three subspecies of sardines in the eastern Pacific:

1) *Sardinops sagax musica*	Chile
2) *Sardinops sagax sagax*	Peru
3) *Sardinops sagax caerulea*	California

However, Saez (1980) showed that there is no reason to distinguish between two subspecies for the Peru Current and based on meristic and morphometric evidence he concluded that the populations of sardines distributed along the coast from Ecuador to Chile comprise a single subspecies, *Sardinops sagax sagax*.

In contradiction to the studies listed above, species synopses for *Sardinops sagax* (De Buen 1960), *Sardinops caerulea* (Ahlstrom 1960), *Sardinops melanosticta* (Tokai Regional Fisheries Research Laboratory 1960), *Sardinops ocellata* (De Jager 1960; Matthews 1960), and *Sardinops neopilchardus* (Blackburn 1960) were presented at the *World Scientific Meeting on the Biology of Sardines and Related Species* which was held in Rome in 1959. The taxonomic sections of these species synopses did not contain a single piece of evidence suggesting that the various forms were indeed separate species and most of the synopses quoted one or more of the above works which state that differences between the various geographically isolated forms are too small to consider them as separate species. Nevertheless they were given their traditional species names; this appears to have been influenced by the fact that at that time a review of *Sardinops* was apparently underway at the Scripps Institution of Oceanography. Ahlstrom (1960) stated that conclusions then permissible from this study indicated that all currently recognized species would be synonymized under the name *Sardinops sagax*; only *neopilchardus* from Australia and New Zealand appeared to merit subspecific rank. This study, apparently by Hubbs, was never published and presently the traditional species names are used, with the exception that the California form is now considered to be *S. sagax* (Robins et al. 1980) and the Russians consider the Kuroshio form to be *S. sagax* (Kenya 1982).

Much of the differentiation of the Clupeidae has been associated with variations in the gill arches in association with adaptations to feeding (Nelson 1967). Nelson suggests that overlapping gill rakers, in some, and the mediopharyngobranchial in all alosins seems to place this subfamily at a higher level of specialization than that of the Clupeinae. Nelson points out that some of the more advanced Clupeinae (*Sardinops* and *Sardina*) have both overlapping gill rakers and a mediopharyngobranchial and that several others (*Sardinella* and *Opisthonema*) have a mediopharyngobranchial. Nelson also suggested that based on similarities in gill arch structure *Sardinops* and *Sardina* are closely related forms and probably should be recombined in a single genus. More recently Whitehead (1970) suggested that Svetovidov's solution (i.e. to recognize five subspecies of *Sardinops*) seemed to be the best.

The history of taxonomy in the sardines suggests that it is easier, and much more acceptable, to describe species than to synonymize them. In spite of the fact that no one has been able to find a characteristic feature with which to separate the various *Sardinops* populations, many workers dismiss contrary evidence such as Svetovidov's (1952) work with comments such as "There is evidence of a 'lumper' at work here!" (Culley 1971) and continue to use individual species names for each of the sardines in each major current system. The fact that the American Fisheries Society (1960) had accepted *Sardinops sagax* as the correct scientific name for the Pacific sardine for more than a decade before Culley's work was published also did not deter him from using the name *Sardinops caerulea* for the California population. Geographic distance rather than meristics, morphometrics or genetics appears to have been the major characteristic utilized in the definition of the presently accepted species of *Sardinops*.

Distribution

One of the most significant features of the sardines is their extensive anti-tropical distribution. *Sardinops*, or *Sardina*, occur in all of the eastern boundary currents and in the western boundary currents of the Indo-Pacific. When their population level within a current system is high they dominate the entire neritic zone of the current system from approximately the area of the west wind drift to the subtropical convergence. When their population level is low their distribution is greatly reduced and they are at times totally absent from areas which are productive fishing areas during periods of high abundance.

Canary Current

It is generally accepted that there are two subspecies of *Sardina* in the North Atlantic and Mediterranean. *Sardina pilchardus pilchardus* occurs off the Atlantic coast of Europe to southern Norway (59°N) (Riedel 1960) and *S.p. sardina* occurs in the Mediterranean and in the Atlantic off North Africa and off the Azores (Fig. 1). However, the distribution of *S.p. sardina* around and north of the British Isles appears to be associated with warm periods and increases in its' abundance (Demir and Southward 1974; Binet 1986; Southward and Boalch 1986). In the past *S.p. sardina* extended to as far south as Cap Blanc (21°N) but it was not abundant south of Cape Bojador (26°N); however, during the mid 1970's there was a large increase in sardines south of Cape Bojador and in association with this increase sardines were taken as far south as the Bay of Goree, Senegal (15°N) (Boely and Freon 1980).

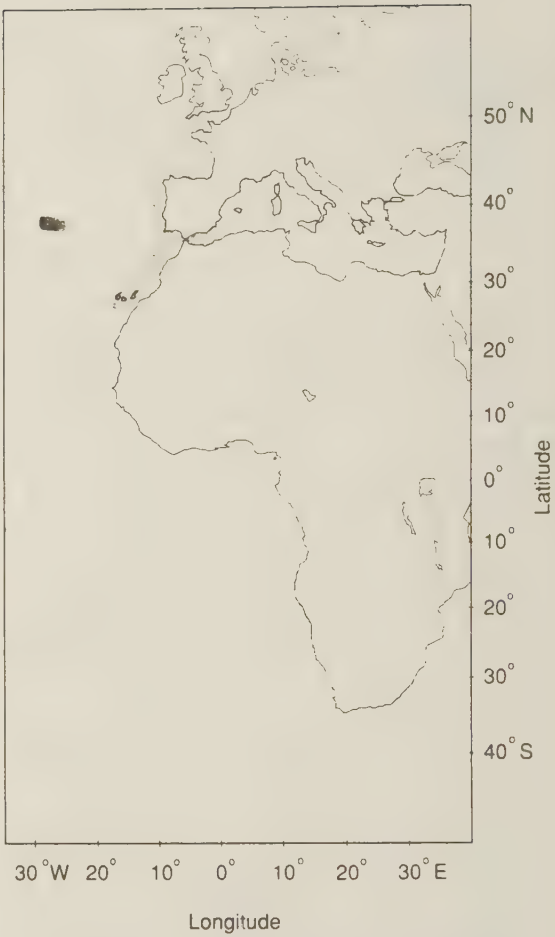

FIG. 1. Distribution of *Sardina* and *Sardinops* in the Atlantic at low abundance (dark shadiong) and the increase in range that occurs at high abundance (light shading).

It is difficult to assess the relative importance of spawning grounds due to the lack of synoptic, large-scale egg and larval surveys covering major segments of *Sardina's* range; however, spawning takes place over a wide portion of *Sardina's* range. In the European Atlantic region spawning appears to be concentrated in the northern Bay of Biscay and the western side of the English Channel (Demir and Southward 1974). Franco and Lago de Lanzas (1976) report spawning grounds off the Cantabric coast in northern Spain, and Atunez, et al. (1973) report spawning off central Portugal. In the Mediterranean "junior stages are found in all sardine areas," according to Larranetta (1960), who lists a large number of spawning areas where young stages are at high concentrations.

Bravo de Laguna et al. (1976), analyzed seasonal migration and maturity stages, and suggest that in the Moroccan area the principal *Sardina* spawning occurs between Cap Juby (28°N) and Agadir (30°N). Little evidence is available for the Saharian region; however, spawning has been reported in the region (Domanewsky and Barkova 1976).

Benguela Current

According to Davies (1956) the range of *Sardinops* in southern Africa extends from Baia dos Tigres, Angola (16°S) around the Cape of Good Hope (35°S) to Durban, South Africa (30°S) (Fig. 1). Spawning grounds are located in the area between Cape Frio (19°S) and Walvis Bay (24°S) (King 1977a) and on the Agulhas Bank (35°S); however, before the decline in landings in the latter area, older sardines also spawned in the area west of St. Helena Bay (32°S) (Shelton 1981).

California Current

In the California Current system *Sardinops* occurs from southern Baja California (23°N) to southeastern Alaska (57°N) and in the Gulf of California (Fig. 2). During the peak in the fishery in the 1930's annual catches in excess of 100 000 tons were taken in Canada; however, with the total collapse of the fishery in the 1950's and early 1960's the range decreased markedly and sardines were virtually absent from the area north of Point Conception (34°N) from the mid-1960's until the early 1980's when a minor recovery of the population resulted in the occurrence of sardines as far north as San Francisco (38°N). Spawning grounds are located from the Southern California Bight (34°N) to southern Baja California (23°N) (Kramer 1970) and in the central portion of the Gulf of California (26–29°N) (Sokolov 1974).

Peru Current

The early literature gives the distribution of *Sardinops* in the Peru Current region from Secchura, Peru (5°S), and around the Galapagos Islands (Hildebrand 1946; Alverson and Shimada 1957) to the Gulf of Arauco (37°S) in Chile (Delfin 1900; Mann 1954). Other authors point out that sardine did not extend south of Coquimbo (30°S) during the late 1950's and early 1960's (De Buen 1958; Brandhorst 1963). During the 1970's sardine abundance increased in the Peru Current region and its range now extends from the equator (0°S) in Ecuador (Garcia 1983) to Chiloe (42°S) in Chile (Serra 1986) (Fig. 2). According to Santander and Flores (1983) spawning grounds off Peru are centered at 5–12°S. Off northern Chile, spawning is centered at 18–26°S and a separate spawning area now occurs from 34–39°S, near Talcahuano (Serra 1983). Paleosediment analyses also suggest that sardines have had population centers in northern Peru (7–10°S) and northern Chile (17–22°S) and a population minimum in central and southern Peru (11–16°S) during much of the Holocene (DeVries and Pearcy 1982).

Kuroshio Current

In the Kuroshio Current region *Sardinops* occurs from south of Japan (29°N) to the east coast of Kamtchatka (54°N) (Tokai Regional Fisheries Research Laboratory 1960) (Fig. 3). During the 1930's when population levels were high the spawning grounds of the Japanese sardine were concentrated in the area around southern Kyushu (29–33°N); sardines from this area migrated northwards throughout the Sea of Japan, along the Pacific coast of Japan to Hokkaido and through the Tsugaru Straits (Nakai 1952). During the 1940's sardines markedly declined in the landings and the fishery was greatly reduced in the northern portion of its range around northern Honshu and Hokkaido, being primarily restricted to the western Sea of Japan and East China Sea; spawning was concentrated in the Sea of Japan northwest of Kyushu (33–35°N) (Nakai 1960). The fishery recovered during the late 1970's and the recovery was associated with recolonization of the spawning grounds around southern Kyushu, a major increase in spawning grounds on the Pacific Coast of Honshu (30–36°N) and the redevelopment of the fishery in northern Honshu and Hokkaido (Tanaka 1983; Watanabe 1983). During the recent period of high abundance, sardines were taken in the Kuroshio Extension at 171°E,

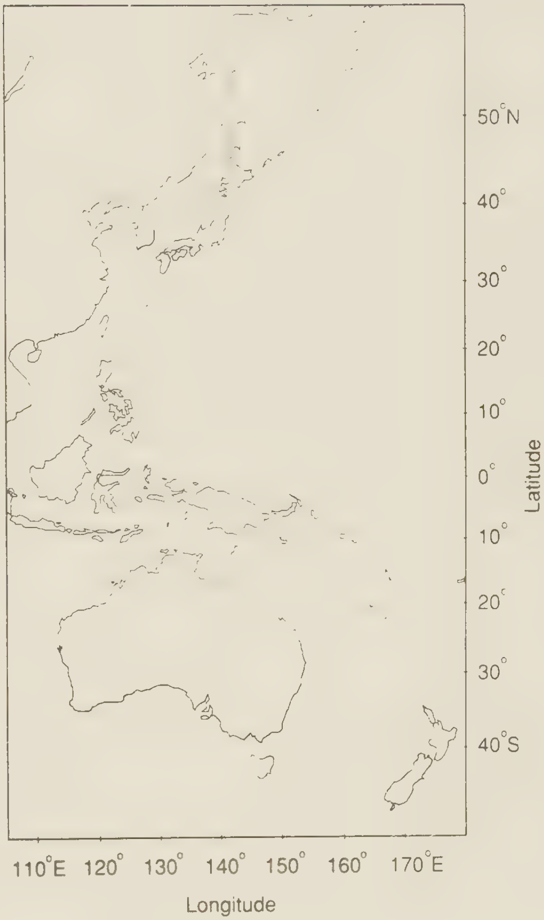

FIG. 2. Distribution of *Sardinops* in the eastern Pacific at low abundance (dark shading) and the increase in range that occurs at high abundance (light shading).

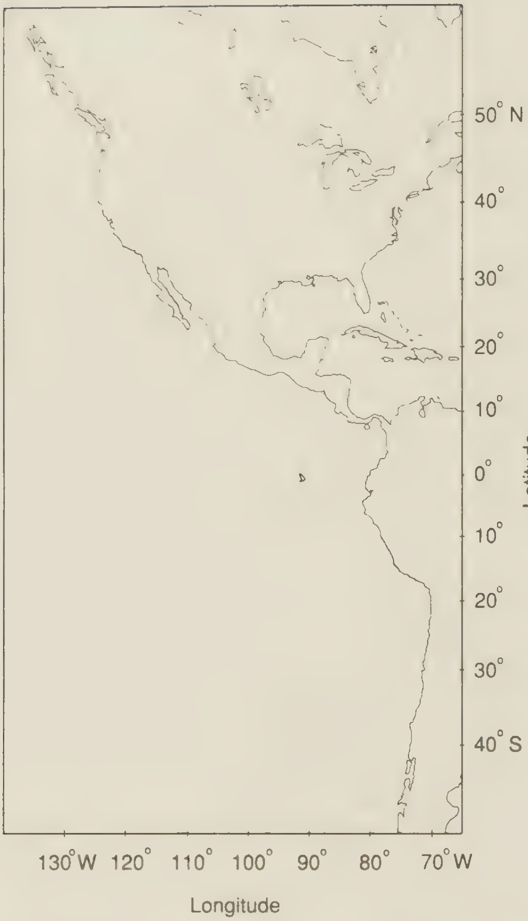

FIG. 3. Distribution of *Sardinops* in the Indo-Pacific at low abundance (dark shading) and the increase in range that occurs at high abundance (light shading).

approximately one third (2800 km) of the way across the Pacific (Kenya 1982).

Australia and New Zealand

Much less information is available on sardine distribution and its variability in Australia and New Zealand than in the other systems due to the lack of a significant fishery. Blackburn (1960) reported the northern limits of the range of sardines in Australia to be 24°S on the west coast and 25°S on the east coast. Their range extends south to southern Tasmania (43°S) and Baker (1972) reported their distribution from 34°S to 46°S in New Zealand (Fig. 3). No extensive egg and larval surveys have been carried out in the Australian and New Zealand region and the distribution of spawning of sardines in the region is not well known; however, Blackburn (1960) shows the breeding range nearly equaling the geographical range in Australia, whereas in New Zealand spawning is concentrated in the area between the North and South Islands near 40°S.

Changes in Geographical Sardine Distribution

The observed variations in the geographical distribution of sardine stocks associated with changes in population size have a similar pattern in each of the current systems where sardines have been heavily exploited (and therefore extensively studied). Sardine spawning grounds have been abandoned as populations decreased in size, or colonized as population size increased, or both. In the Canary Current increases in population size of the Sahara sardine stock was associated with the establishment of a "new stock" in Senegal (Freon and Stequert 1979). The higher latitude distribution of sardines in the Atlantic, i.e. in the English Channel, occurs in association with increased population size (Binet 1986; Southward and Boalch 1986). In the Peru Current increases in the population size in Peru and northern Chile were associated with records of spawning as far north as the equator and with colonization of 'new' spawning grounds in the Talcahauno, Chile region (Garcia 1983; Serra 1983). In the California Current an extreme decrease in the population size resulted in the abandonment of most of the northern range of the California stock. In the Kuroshio Current sardines abandoned much of their range and spawning grounds when the population declined and then several years later recolonized much of their former range and spawning grounds as the population size increased; however, the geographical distribution of biomass and the relative importance of different spawning grounds during the population resurgence was considerably different from that of the previous population maximum (Kondo 1980; Watanabe 1983). The present (1987) spawning range and geographical distribution has returned to very nearly that of the 1930's (T. Kawasaki, Tohoku Univ. Sendai, Japan, pers. comm.).

An outstanding feature of *Sardinops* is the similarity in the timing of extremely large, multi-decade population fluctuations occurring in the Kuroshio, Peru and California current systems (Shuntov and Vasilkov 1982; Kawasaki 1983). As shown above, these fluctuations also resulted in extensive alterations in the geographical distribution of *Sardinops* in each system.

Stock Structure

The stock concept has been interpreted in several different ways in marine fishes. The concept had its inception in studies which demonstrated morphological differences between geographic areas and has become an important organizing principle in the design of research and formulation of management policies by fishery agencies (Cushing 1968). With the realization that morphological variation may merely reflect the response to geographic variation in environmental conditions, and with the development of biochemical methods capable of detecting Mendelian variation, considerable effort has been directed toward using genetic methods, such as protein electrophoresis, to search for discrete stocks (e.g. Allendorf and Utter 1979; Ihssen et al. 1981). The rationale for using genetic methods was that stocks were thought to be reproductively isolated from each other to some degree by distance or by barriers to migration such as warm or cold current systems. Reproductive isolation between stocks is thought to lead to genetic differentiation which is potentially detectable by biochemical methods.

The term "stock" is used differently by different workers. It has been used by some to designate a biologically significant unit; others use the term merely to designate artificial subdivisions of fish into geographic or political areas. For purposes of this review we will use the term stock in its biological sense as an extension of the genetic concept of a population; that is as an aggregation of fish which may or may not be genetically discrete from other aggregations of fish, but one which is isolated, on at least a decadal time scale, from other aggregations.

In each of the major current systems in which sardines occur it is presently believed that there are several stocks. This belief is partially due to the presence of several geographically separated spawning grounds; however, in many cases stocks have been identified by differences in meristic or morphological characteristics such as the number of vertebrae, the number of gill rakers, or differences in body proportions. In most cases these differences appear to be small enough so that it is impossible to determine whether they are caused by developmental responses to variations in the environmental conditions present in the different spawning and nursery grounds or by differences in gene pools. As will be demonstrated later, sardines from high or low latitude regions of different current systems often tend to be more alike in these characteristics than are sardines from high and low latitude areas within a current system. This is not uncommon as a negative correlation between the number of vertebrae and the temperature of their habitat has been found in a number of Clupeids (Muzinic 1960). It also should be noted that it is not possible to use average values such as those derived from meristic or morphometric characteristics to determine the degree of annual admixture between the populations in different spawning areas. In addition, in a few of the current systems some electrophoretic and serological studies of sardine stocks are available.

The following sections review the current knowledge of the stock structure in the regions in which *Sardina* or *Sardinops* occur.

Canary Current

Sardina pilchardus is the most studied of the sardines; an extensive review of the geographical variations in its meristic and morphometric characteristics has been published by Freon and Stequert (1979). The two currently accepted subspecies, which are based parimarily on the number of gill rakers, both occur in the Atlantic. *Sardina pilchardus pilchardus* is generally considered to occur off western Europe, and *S.p. sardina* occurs off North Africa and in the Mediterranean. Determination of the stock structure within the Mediterranean appears to be quite controversial, based on quite small scale geographical features, and a solution was beyond the language skills and endurance of the present authors. In the Atlantic there appears to be some consensus on stock structure.

Bravo de Laguna (1983) points out that *Sardina* extends from Dogger Bank in the North Sea to Cap Vert in Senegal. In this large area Andreu (1969) and Furnestin and Furnestin (1970) distinguished the following geographical stocks.

1) The septentrional Atlantic stock which occurs from the North Sea (57° N) to the Cantabric coast of Spain (43°N). (Vertebrae 52.0)[1]
2) The Iberian or meridional Atlantic stock which occurs from the Cantabric coast to the Straits of Gibraltar (36°N). (Vertebrae 51.2)
3) The Moroccan stock which occurs from Cap Spartel (36°N) to Cap Juby (28°N). (Vertebrae 51.0)
4) The Saharian stock which occurs from Cap Juby (28°N) to Levrier Bay (21°N). (Vertebrae 50.3)

On the basis of the number of vertebrae, electrophoretic differences, and growth differences it has also been suggested that three stocks exist off North Africa (Anon. 1978):

1) A stock near Casablanca (34°N).
2) A stock between Safi (32°N) and Cap d'Anlou (30°N).
3) A stock between Ifni (29°N) and El Ayoun (27°N).

Bravo de Laguna (1983) analysed the results of hydroacoustic surveys and seasonal migrations of sardines off North Africa and concluded that sardines between Safi and El Ayoun might belong to the same stock. He also stated that there was not enough evidence on sardines south of Cap Bojador (26°N) to assess the stock structure in this region.

Analyses of all of the information available on biometric and meristic characters, electrophoretic studies, spawning areas and periods of reproduction, growth studies and distributions observed during hydroacoustic surveys have recently led several workers to suggest that there are three stocks off North Africa (Belveze and Erzini 1983; Rami 1984):

1) Casablanca stock (36°N to 33° 30′N).
2) Moroccan stock (32° 30′N to 27°N).
3) Saharian stock (26°N to 21°N).

Beginning in about 1970 there were increasing amounts of sardines caught along the coast of Mauritania between the latitudes of about 16°N to 26°N and since about 1974 sardines have been taken as far south as Senegal (Anon. 1978). Freon and Stequert (1979) present very convincing evidence that the expansion of the population has resulted in a new stock off Senegal. They also present evidence which places the separation of *Sardina pilchardus* into two subspecies based on the number of gill rakers or vertebrae in doubt. Their fig. 8, which shows the relationships between the number of gill rakers and total length for sardines taken at a wide variety of locations, clearly demonstrates that although there is a strong tendency for the Atlantic, European sardines to have a larger number of gill rakers than the Atlantic, North African and Mediterranean sardines, this is not always the case. For example, sardines taken near Casablanca which are supposedly *S.p. sardina*, the subspecies with the smaller numbers of gill rakers, actually have the largest number of gill rakers of any of the locations. Sardines from their proposed Senegalese stock also have very large numbers of gill rakers. The number of vertebrae appears to be a good characteristic in separating the two stocks of *S.p. pilchardus*; however, the number of vertebrae in *S.p. sardina* taken in most of the Mediterranean areas are intermediate between the two *S.p. pilchardus* stocks and the rest are similar to the Iberian stock or have even fewer vertebrae.

In summary, there appears to be at least four stocks of *Sardina pilchardus* in the northeastern Atlantic. The most likely expansions from the four stock descriptions of Andreu (1969) and Furnestin and Furnestin (1970) given above are the possibility of two Moroccan stocks as suggested by Belveze and Erzini (1983) and Rami (1984), the possibility of a Senegalese stock which is separate from the Saharian stock as suggested by Freon and Stequert (1979) and a stock in the Azores.

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[1] Vertebrae counts were made in different ways by different authors. We have standardized the counts to that suggested by Hubbs and Lagler (1947), (ie. the hypural plate is counted as one vertebrae).

Benguela Current

On the west coast of southern Africa, the Benguela upwelling system may act to some degree as a barrier to migration between sardines off Namibia and those of the southern portion of South Africa. The region of maximum upwelling, which lies between the two regions, may reinforce reproductive isolation between the two regions as it has temperatures which are below the minimal temperature needed for normal sardine larval development (King 1977b). Davies (1956) suggested that there was only a single stock based on small regional differences in the numbers of verbebrae. Newman (1970) concluded, on the basis of tagging experiments, that there was little exchange of individuals between the Walvis Bay fishery in Namibia and the Cape fishery in South Africa. The presence of two widely separated spawning grounds, sharp differences in historical landings in the two areas, and Newman's work led to the general acceptance of the two-stock concept in southern Africa (Butterworth 1983; Crawford et al. 1983):

1) Cape stock (34°S). (Vertebrae 51.2 to 51.4)[2]
2) Walvis Bay stock (22°S).

These stocks have been the subject of three genetic studies using electrophoretic methods. Thompson and Mostert (1974) examined three samples extending from Namibia to the west coast of South Africa for geographic variation at a single locus encoding an esterase enzyme. Allele frequency differences in that study suggested that regional genetic differences may exist between the two areas. Le Clus (1978) searched for geographic variation among five samples taken from the Namibian stock and also detected a significant degree of heterogeneity. In both of these studies, however, there were significant departures from Hardy–Weinberg proportions; these could have resulted from three effects. The first is that the samples may have included individuals from two or more genetically differentiated stocks (the Wahlund effect). The second is that an undetected null or silent allele was present which produced the apparent excesses of homozygotes in the samples. The third is that the phenotypic variation may not have been under simple genetic control. Spurious electrophoretic bands can appear through storage and handling effects (Utter et al. 1979). In the latter two cases any attempt to infer genetic differences between stocks using the data is invalid.

In the third study, Grant (1985b), examined the variation in 30 protein coding loci for six samples extending from 19°N in northern Namibia to 26°S on the south coast of South Africa. Four proteins (excluding esterase) were sufficiently polymorphic to make statistical tests of geographic structure, but no significant differences in allele frequencies were detected among the samples. A gene diversity analysis (Nei 1973) indicated that 99.5% of the total genetic variation that was detected in the samples was contained, on average, within each location. Only 0.5% of the total variation was due to allele-frequency differention among the locations that were sampled. The lack of regional differentiation implies either that there is sufficient migration between the stocks to prevent genetic differentiation or that reproductive isolation between the stocks has occurred only recently, and insufficient time has elapsed for significant differences in allele frequencies to appear. The former explanation is more likely.

California Current

It has been generally accepted that there are at least three stocks of *Sardinops* in the California Current system and a fourth has been proposed (Radovich 1981). Clark (1947) used vertebral counts to demonstrate that sardines in Baja California differed from those further north. Clark and Janssen (1945) and Janssen (1948) used tagging studies to show that there was significant intermixing of sardines between northern Baja California and California and between California, Oregon, Washington and British Columbia. McHugh (1950) found morphometric and meristic differences between sardines in southern Baja California and those to the north. Vrooman (1964) separated the California Current sardines into the following three subpopulations based on serological differences, and he also noted that the number of vertebrae differed between the three subpopulations:

1) Northern stock, from northern Baja California (30°N) to Alaska (55°N). (Vertebrae, 51.44)
2) Southern stock, off the Pacific coast of Baja California (23–30°N). (Vertebrae, 51.36)
3) Gulf of California stock (23–31°N). (Vertebrae, 51.04)

The ranges of the southern and northern stocks appear to overlap seasonally by at least 400 km; southern stock fish were taken as far north as San Pedro, California (34°N) and northern fish were taken as far south as San Quintin Bay, Baja California (30°N); however, it appears that both groups move north or south at about the same time of year with no overlap of the stocks (Vrooman 1964).

In contradiction to Vrooman (1964) recent morphological and biochemical genetic studies have not revealed genetic variation between sardines from central California, the Pacific side of southern Baja California and the Gulf of California (Hedgecock et al. 1985).

Radovich (1962, 1981) postulated that the sardines off the Pacific Northwest (Oregon to Canada) and southern California were somewhat distinct, either genetically or due to a strong tendency for fish to favor areas in which they were born. He pointed out that sardines in the Pacific Northwest were larger and older than those in southern California and that there were differences in the growth patterns on scales from fish in the two areas. The occasional presence of spawning and occurrences of young-of-the-year sardines in the Pacific Northwest (Walford and Mosher 1941) also gives some credence to separation of sardines in the southern California and Pacific Northwest areas. However, the relatively small proportion of young fish in the Pacific Northwest fishery (Radovich 1981) and the rapid movement of tagged fish between the Pacific Northwest and southern California can be used to argue against a separate far northern stock (Janssen 1938). Marr (1960) and Murphy (1966) both rejected the existence of a far northern stock.

Peru Current

The stock structure of sardines in the Peru current system is presently no better understood than that of the other systems and it is further complicated by the recent high population levels which have resulted in a geographical expansion of the range and also apparent recolonization of spawning grounds which were not occupied in the decade prior to the population expansion. There is no conclusive evidence regarding the fishery stock units but there could be three or possibly five stocks based on the spacial pattern of spawning:

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[2] Average vertebrae counts for the Cape stock were given by Baird (1971) as 49.2–49.4. According to P. Shelton (Sea Fisheries Institute, Capetown, South Africa) these counts did not include the urostyle or hyperal plate; for comparative purposes we have therefore increased the counts by two.

1) Northern stock(s), from southern Ecuador (1°S) to central Peru (15°S). The Galapagos Islands may have a separate stock.
2) Central stock, from southern Peru (15°S) to northern Chile (25°S). (Vertebrae 50.87)
3) Southern stock(s), off Coquimbo, Chile (30°S). (Vertebrae 51.15) Off Talcahuano, Chile (37°S).

Supporting evidence for the stock structure of sardines in the Peru Current system is quite limited. Hildebrand (1946) found differences in the number of dorsal rays, 17–20 in Peru vs 15–18 in Chile, and in the relative length of the head, 3.3–3.7 head lengths is the standard length in Peru and 3.48 in Chile. De Buen (1958) gave the following differences between the sardines in Peru and Chile; length of the head 27–28.5% of the standard length in Peru and 25.5–26.1% in Chile, predorsal distance 47–50% of standard length in Peru and 45.1–47.6% in Chile.

Brandhorst et al. (1965) analyzed sardines from Arica, Chile (18°S) and from Coquimbo, Chile (30°S). They found that the mean number of vertebrae were 50.874 ± 0.034 at Arica and 51.153 ± 0.070 at Coquimbo suggesting stock differences may occur between these two regions. The recent expansion of sardines into the Talcahuano region of Chile (37°S) probably occurred from sardines in the Coquimbo region (30°S). The presence of spawning at this new location may indicate that the populations of sardines in these two regions are at least partially independent.

Another feature in the Peru Current is that large geographical dislocations of sardines have been observed in association with El Niño events. Before 1983 the main concentrations of sardines were in northern and central Peru and in northern Chile (Zuta et al. 1983; Serra 1983); however, during the first quarter of the El Niño year of 1983 there was an influx of sardines into southern Peru. It is assumed that these fish were primarily from northern and central Peru, but it is possible that fish from northern Chile also moved into southern Peru as suggested by tag recoveries and spacial distributions shown by hydroacoustic surveys. The Ecuadorian sardine fishery suffered a sharp decline as sardines migrated south into Peruvian waters, apparently avoiding the high water temperatures caused by the same El Niño event (Anon. 1984). Evidence from "normal" years suggests that the abundance of sardines in northern Chile shows a seasonal pattern with peak abundance occurring during the winter spawning season and much lower abundance during the summer and fall (Serra and Tsukayama 1988).

Tagging experiments have shown that during the 1982–83 El Niño there were movements of sardines from both northern and central Peru into Chile (Torres et al. 1984). Maximum movement observed was from approximately 9°S to 30°S (over 2000 km). In other years, tag recoveries suggest that fish move seasonally to and from northern and central Chile (i.e., from 18°S to 30°S) with southward recoveries at a maximum during the summer and northward recoveries at a maximum during the winter.

When the available evidence is viewed as a whole, it is obvious that there is considerable evidence for intermixing of fish from central Peru to Coquimbo, Chile. It is likely that definitive analysis of the stock structure in the Peru Current will only be possible when properly designed biochemical genetic analyses have been carried out.

Kuroshio Current

The number of sardine stocks in the waters associated with the Kuroshio Current system has been the subject of considerable debate The number of stocks proposed to inhabit the area has varied from one (Nakai 1952, 1962) to five or seven (Uda 1960).

According to Nakai (1952), during the period of high abundance in the 1930's the spawning grounds of the Japanese sardine were heavily concentrated in the area around southern Japan (29–33°N); sardines from this area migrated northwards throughout the Sea of Japan, along the Pacific coast of Japan and through the Tsugaru straits. Based on this information he suggested that there was only one stock.

According to Uda (1960), Aikawa and Konisi (1940) considered that there were two stocks.

1) Sea of Japan stock. (Vertebrae 51.75 ± 0.45)
2) Pacific stock. (Vertebrae 51.46 ± 0.55)

Based on the time sequence of catch data, Uda (1960) divided the population into five or seven principal groups for which he suggested that there were spawning grounds corresponding to the various groups but he did not identify the locations.

According to Kondo (1980), after the population size declined in the 1940's it became apparent that there were four subpopulations of the Japanese sardine; however, Kondo presents no documentation for these four subpopulations:

1) Kyushu subpopulation: Spawns along the Western coast of southern Japan) Kyushu to San-in district) and occupies the area from the East China Sea to the Western part of the Sea of Japan.
2) Japan Sea subpopulation: Spawns around the Noto Peninsula (Ishikawa Prefecture) and occupies all of the Sea of Japan.
3) Ashizuri subpopulation: Spawns along the Pacific coast of southern Japan (Kyushu and Shikoku).
4) Pacific subpopulation: Spawns in the Pacific waters along Honshu.

Watanabe (1983) stated that there are two subpopulations on the Pacific side of Japan. However, his statements suggest that the Japanese perspective of subpopulations is quite different from the concept of stock used in this review. For example, he stated that it is assumed that one of the major reasons for the burst in the spawning in the Ashizuri subpopulation was the substantial immigration of parental fish, especially the 1977 and 1978 year-classes from the Pacific subpopulation. He further stated that it is apparent that a substantial amount of the larvae of the Ashizuri subpopulation have been transferred and therefore recruited to the Pacific subpopulation and that intermingling of juvenile and adult fish has widely taken place between the two subpopulations after the expansion of the distribution range in each.

We were unable to find evidence from tagging, biochemical analyses, or traditional taxonomic studies on which to base an analysis of stock structure in the Japanese region. However, the available literature suggests considerable intermixing of sardines throughout the Kuroshio Current region, particularly when abundance is high.

Australia and New Zealand

Blackburn (1960) suggested that two well-separated winter spawning and two well-separated summer spawning regions occur in Australia. On "the assumption that sardines spawn only once a year for a period of a few months only" he proposed that there were four reproductively isolated populations in eastern Australia, possibly two in western Australia and one in New Zealand. In view of recent evidence on spawning frequency of sardines (Alarcon et al. 1984) and the fact that spawning has been observed for extended periods in sardine populations from many areas of the world, our interpretation of Blackburn's (1960) data is that there are four stocks with spawning grounds in the following areas:

1) Western Australia, 27–35°S. (Vertebrae 50.86)[3]
2) Southern Queensland to southern New South Wales, 27–36°S. (Vertebrae 50.89)
3) Victoria, Tasmania, and South Australia, 34–41°S. (Vertebrae 50.83)
4) New Zealand, 35–46°S. (Vertebrae 51.39)

Discussion of Stock Structure

The concept that populations of fishes are subdivided into discrete stocks has a substantial appeal to those responsible for fishery management. Stocks of various species of fishes have been defined by geographic differences in meristic and morphological characters, by regional differences in population parameters, by physiology and behavior, by the results of tagging experiments and by physical oceanographic features (Ihssen et al. 1981; Iles and Sinclair 1982). With the development of such molecular methods as protein electrophoresis and the restriction enzyme analysis of DNA, it became possible to search for genetic differences between the putative stocks which had been defined by non-genetic methods. In the genetic stock concept, stocks are viewed as collections of individuals of a species which freely interbreed. In reality, individuals in the same species do not always freely interbreed because factors external to their genetic systems prevent them from physically mixing. The most important of these are isolation by geographic distance and physical barriers to migration, both of which can lead to some degree of reproductive isolation between local groups of fish. This reproductive isolation may lead to subsequent genetic divergence through natural selection or genetic drift.

The degree to which genetic differentiation among populations is realized varies according to the life history patterns which affect migration and gene flow among populations. Theoretical studies have shown that only a small amount of gene flow is sufficient to prevent genetic differentiation through genetic drift between populations (Wright 1940; Kimura 1955). Populations of freshwater fishes are isolated by physical barriers to a much greater degree than marine fishes. For instance, in freshwater fishes inhabiting lakes or geographically isolated river systems, the amount of the total genetic variation in a species which is due to population differentiation generally ranges between 15 and 20% (Gyllensten 1985). The remaining intraspecific diversity is contained within populations. In anadromous fishes, such as salmon and sea run populations of trouts, between 5 and 10% of the total genetic variation is due to differences between populations (Ryman 1983). Anadromous fishes are less restrained by barriers to migration than are purely freshwater fishes and thus show a greater degree of similarity between populations.

Marine fishes show an even greater degree of similarity between populations because of the large potential for gene flow through unrestrained adult migration or passive drift at the egg and larval stages. In a study of 10 species of near-shore fishes located along the Pacific coast of California and Mexico which had different life-history patterns, Waples (1987) found a negative correlation between dispersal capability and the amount of genetic differentiation among populations. On average, only 4% of the total genetic variation in a species was due to genetic differences among populations. One exception in Waples' study was a species lacking a pelagic larval stage for which 56% of its total variation was due to population differences. In other studies of near shore fishes which spawn benthic eggs less than 2% of the total variation over large areas (1000–3000 km) was due to regional differences (Atlantic herring (*Clupea harengus*) Grant 1984, Ryman et al. 1984; and Pacific herring (*C. pallasi*) Grant and Utter 1985).

Epipelagic or benthic marine fishes which spawn planktonic eggs into coastal current systems show an even greater degree of similarity between populations. Anchovies (*Engraulis*, Grant 1985b), Atlantic mackerel (*Scomber*, Jamieson and Smith 1987), hake (*Merluccius*, Grant et al. 1987), deepwater snapper (*Pristipomoides*, Shaklee and Samollow 1984), damselfish (*Stegastes*, Shaklee 1984), to mention a few neritic marine fishes that have been studied with genetic methods, typically exhibit virtually no genetic differences among locations. Usually much less than 2% of their total genetic diversity is due to regional differences. All of these results clearly demonstrate the homogenizing effect that gene flow has on the genetic stock structure of marine fish populations over large areas.

Grant et al. (1987) have further argued that genetic differences among stocks of marine fishes are unlikely to appear over short periods, on an evolutionary time scale, because genetic drift is unimportant in very large populations. Even for populations which become completely isolated from one another, at least N generations (where N = population size) must pass before any substantial divergence is likely (Kimura 1955). Since the population sizes in the dominant marine fishes tend to be very large, on the order of at least $N = 10^7$ individuals, genetic drift is not an important differentiating force.

Both the foregoing theoretical considerations and previous attempts to find discrete genetic stocks in marine fishes in general, and in southern African sardines in particular, suggest that it is unlikely that sardines within the individual current systems are subdivided into genetically definable stocks.

Speciation

One of the intriguing aspects of the subtropical sardines (*Sardina* and *Sardinops*) is that over much of their range they have few marine Clupeid competitors. In fact, the only other marine Clupeid genus which can be classified as subtropical is *Brevoortia* which occurs in the subtropical northwestern and southwestern Atlantic, the only subtropical, neritic systems in which sardines do not occur. However, the tropical sardine (*Sardinella*) co-occurs with *Sardina* off northwestern Africa and in the Mediterranean.

The subtropical regions are not the only ones with limited Clupeid faunas. There are only two marine sub-polar clupeid

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[3] The number of vertebrae given one higher than that reported by Blackburn (1960) as he did not count the hypural plate.

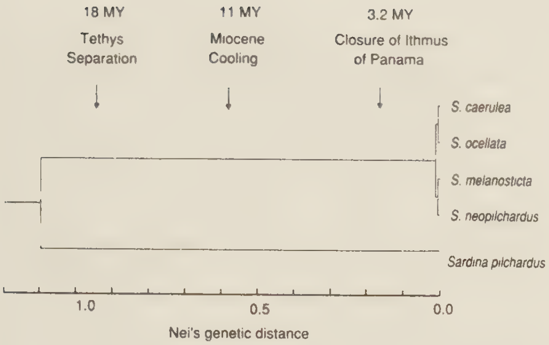

FIG. 4. A UPGMA cluster analysis of Nei's genetic distances (Nei 1972) between geographically isolated populations of *Sardina* and *Sardinops*. Genetic distances are based on data for 29 protein coding loci. Positions of paleo-events are based on an assumed relationship of 19 million years per 1 unit of Nei's genetic distance.

genera, *Clupea* and *Sprattus*, and these have very different distributions, co-occurring only in the northeastern Atlantic and the subpolar portion of South America. We note that according to Whitehead (1964) the taxonomic status of *Clupea bentincki* from South America is still not well resolved. There are, of course, a number of estuarine or anadromous Clupeid populations which are restricted to subtropical and subpolar regions (i.e. *Alosa, Pomolobus, Ramnogaster,* and *Clupeonella*).

Sardinops is unique in that the ecotypes which occur in widely separated current systems exhibit very limited meristic or morphometric diversification, the meristic variations of stocks within the various current systems have a similar latitudinal pattern, and each current system is considered to contain a number of fishery stocks which collectively comprise a very large biomass and occupy a huge geographical area.

It is possible, of course, that the forms in the various current systems look alike but have considerable genetic diversification at the physiological level. Recent biochemical genetic analyses (Grant and Leslie, unpubl. data), however, suggest that the morphological similarity between taxa appears to result from an underlying genetic similarity and not from convergent evolution in response to similar selective regimens in the various current systems.

Grant and Leslie analyzed tissue samples of four of the nominal species of sardines from Japan (*Sardinops melanosticta*), Australia, (*Sardinops neopilchardus*), California (*Sardinops caerula*), southern Africa (*Sardinops ocellata*), and a single species of sardine from Europe (*Sardina pilchardus*). Standard starch gel electrophoretic methods were used to analyze the gene products of 29 enzyme encoding loci. The Mendelian natures of the banding patterns on the gels were inferred according to the criteria outlined in Allendorf and Utter (1979). Allele frequencies were calculated from the resulting genotypic data and used to calculate Nei's (1972) genetic distances between each pair of taxa. Phenetic relationships among the taxa were then inferred using the unpaired group method of cluster analysis (UPGMA) (Fig. 4).

There are two important features of these results. The first is that there is a large genetic distance between the European sardine and the remaining taxa of sardines. The average genetic distance between the European sardine and the remaining sardines was 1.10, a value that is typical of genetic distances between well-differentiated genera in the same family (Thorpe 1982). This confirms the taxonomic separation of the European sardine (*Sardina*) from all of the remaining sardine taxa (*Sardinops*). The second important feature of these results is that there is very little genetic differentiation among taxa in the genus *Sardinops* even though they are separated by very large geographic distances. Genetic distances between the taxa represented by the four samples ranged from 0.002 to 0.009 and are more typical of genetic distances between conspecific populations rather than between species or even between subspecies (Thorpe 1982).

Other than the major division between *Sardina* and *Sardinops*, the cluster analysis of genetic distances did not reveal any apparently meaningful relationships among these taxa. The relationships among the four nominal species of *Sardinops* shown in the phenogram are most likely due to sample effects of the allele frequency data and cannot be taken as reflecting true biogeographic or phylogenetic relationships. Thus the lack of anatomical, morphometric and meristic differences between the *Sardinops* populations in widely dispersed regions of the world is reinforced by a corresponding lack of differences at the biochemical level.

We therefore conclude that *Sardinops* is a monotypic genus as proposed by Svetovidov (1952), and that *Sardinops sagax* is the correct scientific name for the populations in the Agulhas, Benguela, California, Kuroshio, and Peru Currents as well as for the Australian and New Zealand populations. The type specimen is *Clupea sagax* Jenyns, from Darwin's collections, and the description of the species is the original description (Jenyns 1847) plus the material presented by Hubbs (1929) in his description of the genus. *Sardinops melanosticta* (Temminck & Schlegel), *Sardinops ocellata* (Pappe), *Sardinops caerula* (Girard), and *Sardinops neopilchardus* (Steindachner) become synonyms of *Sardinops sagax* (Jenyns).

Biogeography

Discussions of biogeography and speciation are heavily dependent upon the biases of the individuals concerned and before proceeding further we will state our biases in regard to the biogeographic principles under which we are interpreting the sardine data. Firstly, we assume that speciation occurs predominantly as a result of isolation in allopatry (Futuyma and Mayer 1980). This is especially true for epipelagic fishes where it would be difficult to imagine the formation of ecotypes, for instance, within the ranges of species which have extensive migrations. Secondly, allopatric isolation can occur as a result of vicarious events which subdivide a species distribution by superimposing a barrier to migration somewhere within the species range or by dispersal into previously uninhabited areas. Probably the best example of the former with respect to marine fishes is the formation of the Isthmus of Panama. For the latter, the best example is the dispersal of Atlantic or Arctic Ocean fishes into the Pacific, or vice versa, when the Bering Strait opened in the late Pliocene Thirdly, we must assume that the biogeographic relationships among the various sardine taxa have resulted from historical events in the past and are not wholly the result of present oceanographic features.

There are several predictions from population genetics theory and interpretations of biogeographic data in other species that may bear on explaining why there are so few species of sardines. Both theoretical (e.g. Templeton 1980a,b) and paleobiographic (e.g. Jablonski 1986) studies suggest that speciation is more likely to occur in species with highly subdivided population structures, in which the average genetic distance between populations is large, than in species acting like a single panmictic population because of large amounts of gene flow. Theory suggests that genetic changes occur through natural selection and random genetic drift and that change can be much more rapid in small populations than in large populations, and these genetic changes can lead to intrinsic reproductive barriers between populations and to the formation of new species.

Genetic studies of most epipelagic marine fishes (see earlier discussion of stock structure) show that there is generally very little genetic subdivision within the range of a given species. In addition sardines have a number of behavioral characteristics which would tend to reduce their speciation rate. Sardines make extensive migrations and alter their geographical distributions in association with fluctuations in abundance or environmental perturbations. They have extended spawning seasons with multiple spawning; some spawning is observed all year in many of the warmer spawning grounds. Thus there is extensive opportunity for interbreeding between fish from different geographical areas within a current system. In addition, as previously mentioned, sardines have extremely large populations. Sardines must therefore be included in the category of species that are not likely to speciate within an individual current system. Thus we do not see sympatric or parpatric species of sardines which can be interpreted to have arisen in situ.

On a broader geographic scale there are two problems requiring explanation. One is to explain the major phylogenetic subdivision between the European sardine (*Sardina pilchardus*) and the remaining taxa in the genus *Sardinops*. The other is to explain why the populations of *Sardinops* in widely separated current systems are genetically so similar.

Before attempting to answer these two questions, it would be useful to put the biogeographic and speciation events of these taxa into a temporal context. A genetic distance can be used to estimate in a rough way the time since divergence between two related taxa (Grant 1987). Empirical calibrations of genetic distance suggest that a Nei genetic distance of 1.0 is approximately equal to 19 million yr of divergence time. However, comparisons of genetic distances between pairs of related fish taxa separated, for instance, by the Isthmus of Panama 3.1 million yr ago, show that there is a large error associated with any estimate of time. Therefore it is better to use the estimate of genetic distance along with its standard error to estimate a period of time when divergence was most likely. For the *Sardina–Sardinops* split with $D = 1.10$ (SE 0.26) this period of time extends from 16 to 26 million yr before the present; or from the end of the Oligocene to the mid-Miocene. For the various *Sardinops* splits the average D value was 0.005 (range 0.002–0.009) and the average standard error was 0.004 (range 0.002–0.008). Using the average D value and the average standard error the time of divergence of the *Sardinops* populations would have occurred from 19 000 to 171 000 BP. Both dates are in the late Pleistocene. The last glacial period is considered to have peaked about 18 000 BP and the last interglacial period was about 125 000 BP.

Given the present-day location of *Sardina pilchardus* and the apparent length of time that they have been separated from *Sardinops*, we suggest that the closure of the Tethys Sea in the late Oligocene by the colliding continental plates of Laurasia and Africa (King 1983) served as a vicariant event leading to the separation of the ancestral sardine taxa into two isolated populations. *Sardina* was then derived from the North Atlantic population and *Sardinops* from the Indo-Pacific population.

Sardina is presently restricted to the subtropical portion of the northeastern Atlantic and the Mediterranean. The absence of *Sardina* from the northwestern Atlantic, if indeed it ever existed there, could be explained by local extinction during Pliocene or Pleistocene cooling. During periods of cooling the North Atlantic was characterized by large-scale intrusions of cold polar water and during the Pleistocene much of the North Atlantic was repeatedly covered by an ice sheet (Kellogg 1980). Latitudinal isotherms were much compressed during these cooling episodes (CLIMAP 1976) and habitat alterations could have easily led to the extinction of *Sardina* in the northwestern Atlantic. The dispersal capability of *Sardina* is apparently not great enough for it to have made the upstream, westward transit across the mid-latitude Atlantic since the last glacial maxima; nor has its temperature tolerance permitted it to colonize the northwestern Atlantic by westward advection around the polar, northern rim of the North Atlantic or along the North Atlantic equatorial current.

The task of explaining the biogeographic origins and distribution of *Sardinops* is much more difficult. The minor genetic distances between populations in different current systems suggest two general hypotheses:

1) There is ongoing migration between the various current systems which keeps the populations so genetically similar.
2) *Sardinops* achieved its present distribution as the result of Pleistocene climatic changes, in which case there were probably exchanges between current systems at some time during each glacial cycle.

Before developing these hypotheses it should be noted that the earliest time that *Sardinops* could have achieved its present distribution was probably during the late Miocene. The middle Miocene fish fauna of California is quite well known and Jordan (1921) points out that, with few exceptions, the middle Miocene fauna is similar to the present subtropical fauna of California. One of his exceptions is "There are no anchovies, sardine, or true herring, the numerous herring-like forms being all of rare or extinct types." We note that the striations on the opercular bones of *Sardinops* and *Sardina* make them particularly easy to identify as fossils. It should be noted that Fitch (1969) found the otoliths of the northern anchovy, *Engraulis mordax*, and the Pacific herring, *Clupea pallasi*, but not *Sardinops* in three Pliocene deposits and numerous Pleistocene deposits. The earliest recorded occurrance of *Sardinops* in the California Current region is from Holocene sediments off Vancouver Island which were dated between 8 850 and 9 840 yr BP (Casteel 1975). The earliest recorded occurrance of *Sardinops* in the Peru Current region is not much earlier; (i.e. between 11 400 and 11 700 yr BP, DeVries and Pearcy 1982). However, we were unable to find any studies of the Miocene–Pleistocene marine fish fauna of this region.

To evaluate the first hypothesis it is necessary to evaluate the probability of exchanges of sardines between current systems under the present climatic conditions. Sardines are highly migratory, epipelagic plankton feeders and it is certainly within the realms of possibility that they could simply swim across an ocean. For example, tagged sardines have made one-way migrations between southern California and Canada (1850 km) in as little as 103 d (Jannsen 1938). On the other hand they do not occur in the northwestern or southwestern Atlantic.

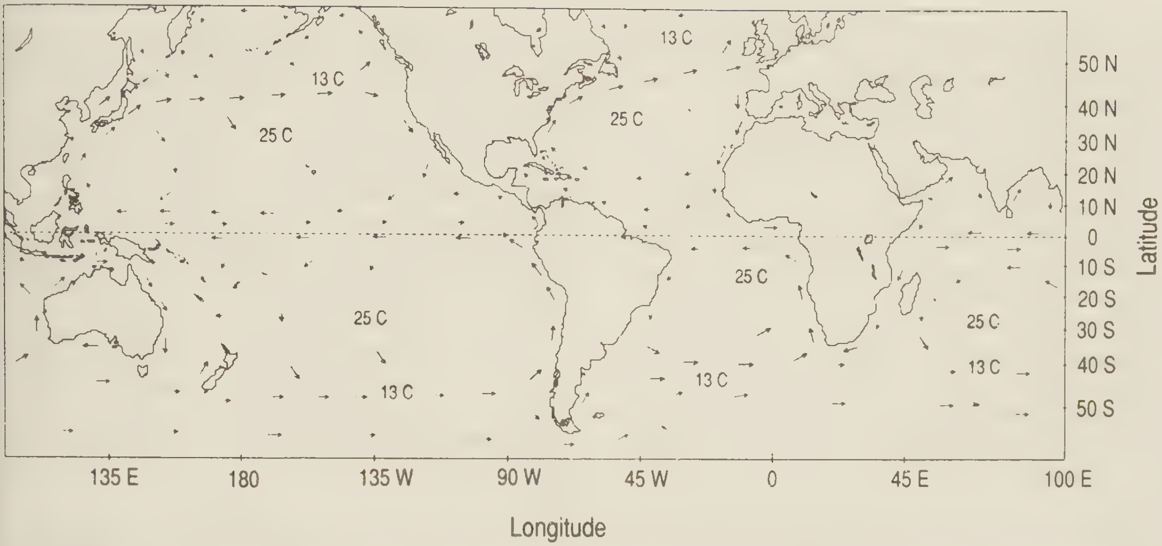

FIG. 5. Major ocean circulation features and area with summer sea surface temperatures between 13 and 25°C (shaded). Based on charts in Sverdrup et al. (1942).

The biomass levels of sardines within each of the major current systems for which population estimates exist, have at times exceeded several million tons. At these biomass levels there are undoubtedly millions of larval and juvenile sardines swept offshore and lost to the neritic populations each year. It is therefore possible that sardines could be passively advected from one current system to another.

The temperature tolerance of adult *Sardinops* is from 7 to 27°C (Tokai Regional Fisheries Research Laboratory 1960; Ahlstrom 1960) and most spawning occurs at temperatures of 13–17°C (Ahlstrom 1960). In all of the regions in which it occurs the high and low latitude edges of the normal range of *Sardinops* (Fig. 1–3) are well described by the summer 13 and 25°C isotherms (Fig. 5). This is well within the range of sea surface temperature (SST) occurring in the mid-latitudes but SST at low and high latitudes (Sverdrup et al. 1942) is near or exceeding lethal temperatures for sardines. Of course sardines could feasibly avoid the high equatorial SST by staying in the thermocline to avoid thermal stress. However, the interaction between the increased metabolic rates that would occur at higher temperatures and the lower food availability which occurs in tropical waters would be a severe limitation to sardine survival in equatorial and central water mass regions.

The most likely exchange of sardines between current systems, with the present climatic conditions, would appear to be a mid-latitude crossing from a western boundary current to an eastern boundary current via one of the west wind drift regions. Recent research on the near surface currents of the North Pacific, using drifting buoys, has shown that the average transit time across the North Pacific going east in the mid-latitudes and west in the equatorial regions is approximately the same, 700 d (McNalley et al. 1983). Sardines often live for up to 10 yr and 5-yr-old fish are quite common. It is thus feasible that there could be passive advective exchanges within an ocean basin gyral system. The major limitations to this type of exchange would appear to depend on the availability of food and encounters with predators. Sardines are essentially planktivorous species which feed on both phytoplankton and zooplankton. McGowan (1972) has described the biogeography of the major zooplankton faunal assemblages in the Pacific. He describes a ''transition zone'' fauna which is distributed along the warm side of the subarctic convergences associated with the west wind drift. It is obvious from a comparison of the distributions of McGowan's faunal assemblages with that of *Sardinops* that, in the Pacific, *Sardinops* populations are centered in the neritic boundaries of the transition zone fauna. This implies that sardines could remain within the transition zone fauna if, for example, they were advected eastward from the Kuroshio Current to the California Current via the North Pacific Current (i.e., the west wind drift region) but not if they were advected westward from the California Current to the Kuroshio Current via the North Pacific Equatorial Current or via the Alaska and Oyashio Currents (Fig. 5).

In this regard, Kenya (1982) has reported finding commercial quantities of sardines along a large portion of the Kuroshio extension; sardines were taken as far east as 171°E. This is approximately 2800 km from the spawning grounds of southern Honshu and approximately one third of the way across the Pacific. Kenya also found young-of-the-year sardines as far east as 166°E in July. Thus it is likely that during the Holocene there has been frequent eastward, advective mixing of sardines from the Kuroshio Current to the California Current via the west wind drift region and, by analogy, between the southern African, Australian, New Zealand, and South American populations.

Conversely westward, advective exchange via the equatorial currents would be very unlikely as it would have to occur at near lethal temperatures and within zooplankton faunas in which sardines do not normally occur. Westward, advective exchange via the Alaska Current would presently be impossible as temperatures are near, and seasonally below, the sardine's temperature tolerance range, and there is no comparable subpolar gyre in the southern hemisphere. Westward mid-latitude exchange, via the northern and southern hemisphere west wind drift regions, would also be very unlikely as it would have to occur against the prevailing currents (Fig. 5).

Exchange of sardines between the southern and northern hemispheres would also appear to be very difficult as present sea surface temperatures near the equator are higher than those in which sardines normally occur and, for the most part, the present large scale circulation patterns would tend to hinder exchanges between the northern and southern hemispheres. If transequator exchanges are possible under the present climatic conditions they would be more likely to have occurred on the eastern edges of the oceans rather than the western edges . There are two principal reasons for this; the eastern edges of the tropical oceans are cooler than the western edges and the eastern boundary currents advect cool (sardine rich) water towards the equator whereas the western boundary currents advect warm (sardine poor) water away from the equator.

The most likely area for transequator exchanges with the present climatic conditions is the Eastern Tropical Pacific. In the eastern Pacific *Sardinops* occurs to southern Baja California (24°N) in the California Current and to the equator in both Ecuador and the Galapagos Islands. *Sardinops* does not presently occur in the Eastern Tropical Pacific; however, it can at times survive there as fishing vessels have successfully transported it from the Galapagos Islands to the Central American tuna fishing grounds as live bait (Alverson and Shimada 1957). Present SST in the Eastern Tropical Pacific (Sverdrup et al. 1942) is near the lethal limit for sardines; however, the prevailing near-shore currents would favor dispersal from the Peru Current to as far north as southern Mexico. Seasonally, currents are favorable as far as 28°N in the Gulf of California (Baumgartner and Christensen 1985). Conversely southern dispersal from the California Current to the Peru Current would be hindered by the prevailing currents.

The second area in which transequator exchanges might occur with the present climatic conditions is in the Guinea Current region. *Sardina* presently occurs as far south as 15°N in the Canary Current and *Sardinops* occurs as far north as 16°S in the Benguela Current. Sea surface temperatures over most of the Guinea Current region (Sverdrup et al. 1942) are near or above the lethal limits for sardines. The region has somewhat lower SST in August with SST over some of the area below 25°C: however, at this season SST in the area between the Canary and Guinea currents is above 27°C. The prevailing current in the Benguela and Canary Currents is equator-ward. Sardines could therefore possibly be advected to the equator; however, once across it they would have 15 degrees of latitude to cross, against the prevailing currents at near-lethal SST, before reaching sardine habitat in the opposite hemisphere. Thus transequator exchanges in the Atlantic appear to be impossible for either *Sardina* or *Sardinops*.

The second hypothesis is supported by the fact that the apparent time of divergence between populations in the different current systems is placed in the Pleistocene, a time of both global oceanic cooling and warming that would have enhanced migration from one current system to the other. We note that the genetic distance of 0.003 between the Japanese and Californian sardine populations is on the same order of magnitude or less than genetic distances observed between eastern and western Pacific ocean populations of Pacific herring, *Clupea pallasi* (Grant and Utter 1984), and Pacific cod, *Gadus macrocephalus* (Grant et al. 1987).

Eastward exchange between western and eastern boundary currents during the Pleistocene would have been possible with the same explanations as those given above for the present climatic conditions. It is likely, however, that conditions are more favorable at some stages in the glacial cycle than at others. Westward exchange during glacial maxima via the equatorial currents would have been nearly as unlikely as at present as there is little temperature difference in the tropics between glacial maxima and minima (CLIMAP 1976). However, there is considerable difference between temperatures at glacial maxima and minima in the subpolar regions (CLIMAP 1976) and paleosediment analyses show that the North Pacific subpolar gyre is an area with maximum faunal changes between glacial maxima and minima (Ruddiman 1985). Westward exchange may, therefore, have been possible in the North Pacific via the Alaska Current when conditions were warmer than at present (i.e., in the Pliocene or during extreme interglacial periods during the Pleistocene).

The evidence discussed earlier suggests that with the present climatic conditions transequator exchanges of sardines are not possible anywhere except in the Eastern Tropical Pacific, and they would have to be considered very unlikely even there. However, recent evidence from oxygen isotope and radiolarian analyses of ocean cores suggests that at the last glacial maximum (18 000 yr BP) the August 25°C isotherms were displaced southwards to southern Mexico (18°N) and northwards to southern Costa Rica (8°N) and maximum mean SST in the eastern tropical Pacific was only 26°C (Ruddiman 1985). Jones and Hassen (1985) suggest that contact between the Tethys-derived coral fauna in the Caribbean and Tropical Pacific was lost in the late Pliocene, following development of the Panama land bridge, and the virtual extinction of the eastern Pacific coral reef fauna ensued during Pleistocene glaciations. There is, therefore, considerable evidence that implies that climatic conditions in the Eastern Tropical Pacific would have been cool enough to allow *Sardinops* from the Peru Current to cross to the California Current during Pleistocene glacial maxima.

In summary we suggest:

1) Eastward, advective exchange of *Sardinops* between western and eastern boundary current systems via the west wind drift regions and within the transition zooplankton faunal zones is possible with the present climatic conditions.
2) Westward, advective exchange of *Sardinops* from the California Current to the Kuroshio Current via the subpolar gyre is not presently possible, but it would have been possible during the late Miocene and early to mid-Pliocene when sea surface temperatures were warmer than those that have existed since the onset of northern glaciation in the late Pliocene. It may also have been possible during extreme interglacial maxima.
3) Westward, advective exchange is and was not possible via the equatorial currents due to their high SST and different zooplankton fauna.
4) Westward exchange, against the prevailing current, is and was not possible within the west wind drift regions.
5) Trans-equator exchange is only possible in the eastern Pacific and is most likely to occur during glacial maxima.

If the above statements are accepted, then it can be postulated that the present distribution of *Sardinops* was derived from the Indo-Pacific segment of the original Tethys sardine population. *Sardinops* is most likely to have achieved its present distribution by first dispersing from the southern Indian Ocean to

Australia, New Zealand, and Pacific South America via the southern hemisphere west wind drift. The absence of *Sardinops* in the southwestern Atlantic Ocean can be explained by the fact that *Sardinops* from the Benguela Current would have to move against the west wind drift current to colonize the region and *Sardinops* from the Pacific could not reach the region as the southern tip of South America extends into water that is too cold for *Sardinops*.

The present southern hemisphere distribution was probably achieved by the late Miocene or early Pliocene, a period when ocean temperatures were decreasing and oceanic productivity was increasing. In the eastern Atlantic, paleo-oceanographic reconstructions show that, although there was considerable cooling in temperate areas, Pleistocene equatorial waters remained nearly as warm as present day equatorial waters (Thunell and Belyea 1982). Indeed, there is no evidence to show that *Sardinops* (or *Sardina*) crossed the equator in this region. The colonization of the North Pacific apparently did not occur until after the closing of the Isthmus of Panama and the onset of extensive northern hemisphere glaciation in the late Pliocene; it is most likely to have occurred in the Pleistocene when the minimum ocean temperatures associated with a glacial maxima would have resulted in climatic conditions which would most favor the dispersal of *Sardinops* from the Peru Current to the California Current. There is a possibility that *Sardinops* achieved its present distribution by reaching the Kuroshio Current, via the North Pacific subpolar gyre, in the late Pliocene; however, this probably occurred during an extreme interglacial period in the Pleistocene.

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The South Pacific Oceanic Horse Mackerel *(Trachurus picturatus murphyi)* Fishery

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Abstract

The horse mackerel fishery of the South Pacific currently dominates the world's catch of horse mackerels. The rapid increases in catches of horse mackerel by South American purse seine fleets and the distant water USSR trawl fleet are discussed and the geographical expansion of the trawl fishery is shown utilizing ship surface weather observations.

Due to disagreement on the taxonomic identity of the species which supports the fishery, a review of the world's *Trachurus* was made. The results of this review show that neither of the eastern Pacific forms of *Trachurus* merits full species rank. It is concluded that both are subspecies of the oceanic horse mackerel *(Trachurus picturatus)*; *T.p. symmetricus* in the northeastern Pacific and *T.p. murphyi* in the southeastern Pacific. It is further suggested that it is likely that the range of *T.p. murphyi* extends clear across the southern hemisphere west wind drift region (i.e., from the South Atlantic to Chile).

Resumen

Las pesquerías de jurel en el Pacífico Sur dominan actualmente las capturas mundiales de jureles. Se discute el rápido incremento en las capturas de jurel por las flotas cerqueras sudamericanas y la flota arrastrera soviética que opera en aguas distantes y se muestra la expansión geográfica de las pesquerías de arrastre mediante el empleo de observaciones del clima efectuadas por los barcos.

Se hace una revisión de los *Trachurus* del mundo, en vista de los desacuerdos en la identidad taxonómica de las especies que soportan las pesquerías. Los resultados de esta revisión muestran que ninguna de las formas de *Trachurus* del Pacífico Oriental amerita plenamente la jerarquía de especie. Se concluye que ambas son subespecies del jurel oceánico *(Trachurus picturatus)*; *T.p. symmetricus* en el Pacífico Nororiental y *T.p. murphyi* en el Pacífico Suroriental. Se sugiere además que es probable que el rango de *T.p. murphyi* se extienda a través de la región con vientos del oeste del hemisferio sur (desde el Atlantico Sur a Chile).

Introduction

Horse mackerels, of the genus *Trachurus*, are a widespread group occurring in nearly all of the temperate and subtropical, neritic regions of the oceans and they have extensive, but poorly understood, oceanic distributions in several regions. They also occur in a number of tropical neritic regions. The taxonomy of the group is in considerable flux and their extensive distribution is undoubtedly, at least partially, the cause of the present taxonomic confusion: forms which are very similar in morphology and meristics, but widely separated geographically, are assumed, a priori, to be separate species by many workers.

Over the last two decades the horse mackerels have had one of the largest increases in the world's fish catch. Landings rose from 1.2 x 10^6 tonnes (t) in 1965 to 3.9 x 10^6 t in 1984. In 1965 catches of horse mackerel were principally from the northern hemisphere (0.80 x 10^6 t); however, the increase in catches has been entirely the result of developing fisheries in the southern hemisphere (Fig. 1A). Although horse mackerel occur in much of the world ocean, the bulk of its catches, and supposedly biomass, is concentrated in the eastern boundary currents (Fig. 1B).

Regionally the catches of horse mackerels have exhibited tremendous changes over the last two decades (Table 1). In 1965 half of the world catch of *Trachurus* came from the northwestern Pacific (0.55 x 10^6 t) and the rest was primarily taken in the northeastern Atlantic (0.22 x 10^6 t) and southeastern Atlantic (0.31 x 10^6 t). By the early 1970s catches from the northwestern Pacific had declined greatly, whereas catches from the other two regions had significant increases. Catches reached a maximum of 0.91 x 10^6 t in the northeastern Atlantic in 1973 and a maximum of 0.97 x 10^6 t in the southeastern Atlantic in 1978. Most of these increases in catches were due to the development of distant-water trawl fisheries off North and South Africa by European nations.

Development of the South Pacific Fishery

The most significant change in the world's horse mackerel catches occurred as the result of the development of the southeastern Pacific fishery which rose from 0.015 x 10^6 t in 1965 to a maximum of 2.32 x 10^6 t in 1984 (Fig. 1C). The South Pacific fishery was developed in the early 1970s by Chilean purse seiners forced to alter their fishing strategies due to the collapse of the

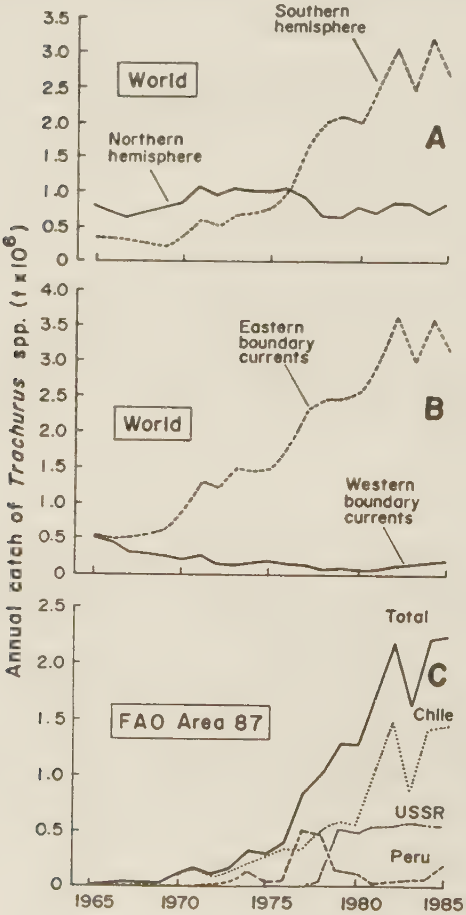

Fig. 1. Catches of *Trachurus* spp., 1965-1985. A. World catches, by hemisphere. B. Catches, by ecosystem type. C. Catches in FAO Area 87, by country.

Fig. 1. Capturas de Trachurus *spp., 1965-1985. A. Capturas mundiales, por hemisferios. B. Capturas, por tipos de ecosistemas. C. Capturas en el area 87 de FAO, por paises.*

Table 1. World catch of *Trachurus* by FAO statistical area (x 10^2 t).
Tabla 1. Captura mundial de Trachurus *por áreas estadísticas de FAO (x 10^2 t).*

OCEAN	Indian		N. Pacific		S. Pacific		N. Atlantic		S. Atlantic		Total
	E.	W.	E.	W.	E.	W.	E.	W.	E.	W.	
FAO AREA Year	51	57	61	67 + 77	81	87	31	27 + 37 + 34	41	47	
1965	0	0	5,534	303	0	153	0	2,175	2	3,121	11,288
1966	0	0	4,872	187	1	219	0	1,873	4	3,024	10,180
1967	0	0	3,342	174	5	295	0	2,779	37	2,492	9,124
1968	0	0	3,145	254	6	269	0	3,513	13	2,063	9,263
1969	0	0	2,858	236	3	227	0	4,25	3	1,838	9,688
1970	31	0	2,221	217	3	1,167	0	5,853	10	2,318	11,820
1971	4	0	2,834	272	138	1,676	0	7,626	4	3,992	16,546
1972	21	0	1,565	232	187	1,113	0	7,721	1	3,647	14,487
1973	16	0	1,308	94	157	1,644	0	9,067	2	4,818	17,106
1974	19	0	1,685	100	192	3,235	0	8,287	15	3,455	16,988
1975	45	0	1,932	204	138	2,991	0	7,855	5	4,534	17,704
1976	50	0	1,360	184	163	3,964	0	8,897	13	6,095	20,726
1977	349	0	948	501	175	8,480	0	7,792	17	7,511	25,773
1978	96	0	640	324	112	10,144	0	5,525	20	9,656	26,517
1979	79	0	932	166	75	12,873	0	5,112	6	7,672	26,915
1980	35	0	567	216	63	12,806	0	7,076	9	6,941	27,713
1981	24	0	716	159	116	17,403	0	6,054	14	7,725	32,211
1982	37	0	1,196	263	147	21,996	0	6,966	7	7,978	38,590
1983	64	0	1,461	187	207	16,682	0	6,739	4	7,464	32,808
1984	86	0	1,468	109	403	23,240	0	5,437	3	7,973	38,719
1985	83	0	1,738	97	413	21,488	0	6,487	4	4,472	34,782

anchoveta fishery in 1972-1973 (Table 2). Chilean landings of horse mackerel reached 0.5 x 10^6 t in 1978 and, except for the El Niño year of 1983, have exceeded 1.4 x 10^6 t since 1981. In the early 1970s Peru also began to develop a purse seine horse mackerel fishery; however, this fishery has not achieved the production of the Chilean fishery and with the exception of 1977-1978, when landings were near 0.5 x 10^6 t, landings have averaged less than 0.1 x 10^6 t.

Both the Chilean and Peruvian horse mackerel fisheries are neritic fisheries with catches almost exclusively coming from their respective 200 mile economic zones. The Chilean fishery started in northern Chile, in the Arica-Antofagasta region and expanded to central Chile in the late 1970s (Serra 1987). During the 1980s the Chilean landings have been about equally divided between the Arica-Antofagasta region (18-24°S) and the Talcahuano region (37°S); landings in the Coquimbo region of central Chile (30°S) have been an order of magnitude less than in the other two regions (Serra 1987). Fishing areas for the Peruvian catches are not well-documented in the available literature.

Table 2. Southeastern Pacific *Trachurus* catch by country (FAO Area 87; x 10^2 t).
Tabla 2. Captura de Trachurus *en el Pacífico Suroriental por países (Area 87 de FAO; x 10^2 t).*

	Chile	Peru	Ecuador	USSR	Other	Total
1965	127	26	0	0	0	153
1966	176	43	0	0	0	219
1967	264	31	0	0	0	295
1968	241	28	0	0	0	269
1969	185	42	0	0	0	227
1970	1,120	47	0	0	0	1,167
1971	1,584	92	0	0	0	1,676
1972	870	188	0	55	0	1,113
1973	1,216	428	0	0	0	1,644
1974	1,944	1,292	0	0	0	3,236
1975	2,612	379	0	0	0	2,991
1976	3,423	542	0	0	0	3,965
1977	3,408	5,049	0	0	22	8,479
1978	5,001	4,625	0	492	25	10,143
1979	5,975	1,516	0	5,322	60	12,873
1980	5,622	1,234	0	4,944	1,004	12,804
1981	10,609	379	0	5,546	868	17,402
1982	14,946	450	0	5,554	974	21,924
1983	8,652	679	249	5,910	792	16,282
1984	14,263	768	100	5,706	1,327	22,164
1985	14,569	1,843	6	5,639	398	22,455

In 1978, trawlers from the USSR began fishing for horse mackerel offshore of the 200 mile limits of Peru and Chile and during the period 1979-1985 they have annually taken between 0.49 and 0.59 x 10^6 t in the offshore area (Table 1). The development and distribution of this distant water trawl fishery is well documented in the positions of the trawlers as reported in international meteorological observations. At the beginning of the fishery (1979) the reported positions were spread out in a band along the coast, outside of the 200 mile zones (i.e., between 80°W and 90°W from 10°S to 45°S in Fig. 2A). By 1983 reports show the fishery was concentrated off southern Chile at about 80°W and 40°S (Fig. 2B); however, there were also a considerable number of reports along 85°W north of the area of concentration. There was an absence of reports within Chile's 200 mile zone; Chile also has 200 mile zones around San Felix Island and Juan Fernandez Archipelago. By 1985, in addition to a distribution of reports similar to 1983, the reports show that the fishery extended westward along the west wind drift between 39 and 45°S (Fig. 2C).

To evaluate the seasonality of the Soviet trawl fishery, the meterological reports were limited to Soviet vessels and to 1984-1987, the period when the fishery was operating in the offshore west wind drift region. During the austral spring (October-December) the meterological reports are furthest to the north with reports concentrated between 34-41°S and 78-92°W (Fig. 3A). Reports are noticeably absent in the 200 mile zones around San Felix Island (26°S, 80°W) and the Juan Fernandez Archipelago (33°S, 80°W) but there are reports in international waters between the two zones and between the San Felix Island 200 mile zone and the continental 200 mile zone. During the austral autumn (April-June) the reports are concentrated in two regions

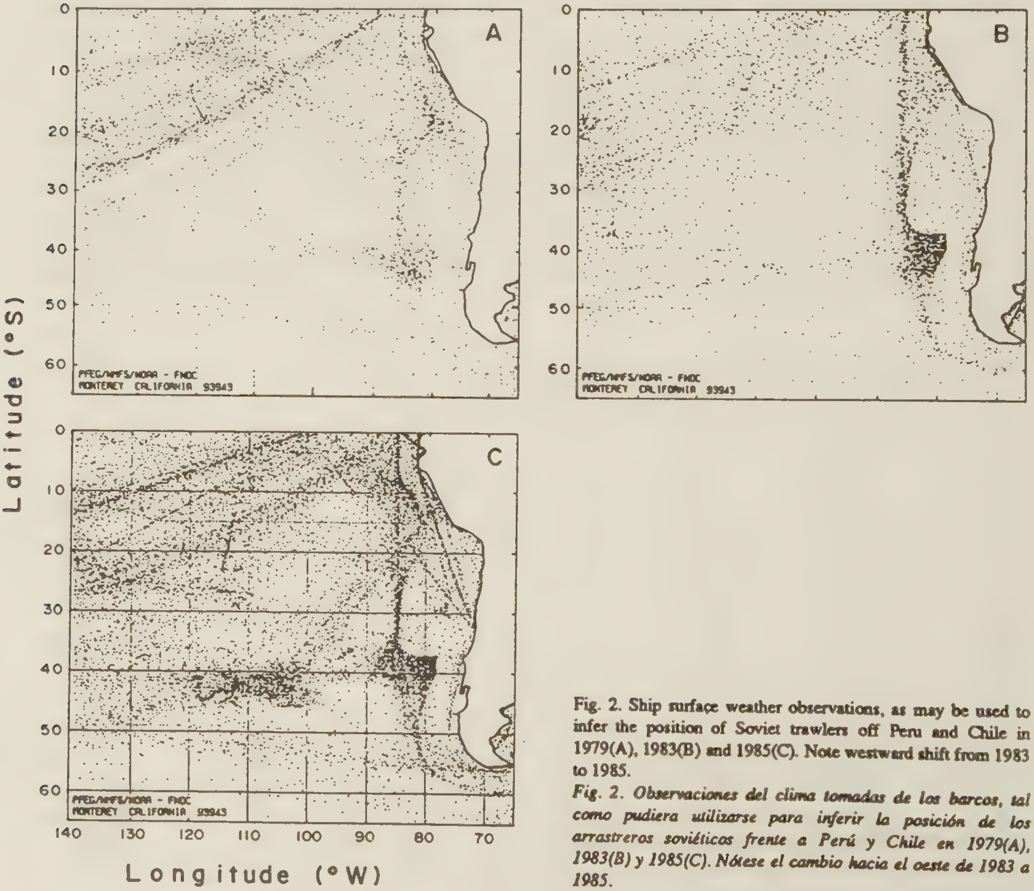

Fig. 2. Ship surface weather observations, as may be used to infer the position of Soviet trawlers off Peru and Chile in 1979(A), 1983(B) and 1985(C). Note westward shift from 1983 to 1985.

Fig. 2. *Observaciones del clima tomadas de los barcos, tal como pudiera utilizarse para inferir la posición de los arrastreros soviéticos frente a Perú y Chile en 1979(A), 1983(B) y 1985(C). Nótese el cambio hacia el oeste de 1983 a 1985.*

(Fig. 3B). The first is about five degrees south of the spring concentration (i.e., between 39-45°S and 79-90°W) and the second is much further offshore (39-45°S and 100-120°W). In both spring and autumn there are also considerable numbers of reports in the offshore region extending toward New Zealand.

The South Pacific distribution of the meterological reports from the Soviet trawl fleet suggests that, in the offshore region, horse mackerel are concentrated along the South Pacific subtropical convergence and that they seasonally move north and south with the convergence. It appears that the horse mackerel are able to complete their entire life cycle in the South Pacific subtropical convergence; independent of the neritic zone. Evseenko (1987) reported several larvae and a juvenile in the South Pacific convergence and Bailey (1989) shows that the horse mackerel spawns across the South Pacific from New Zealand to Chile. Bailey found juvenile horse mackerel along the subtropical convergence from 128°W to 166°W.

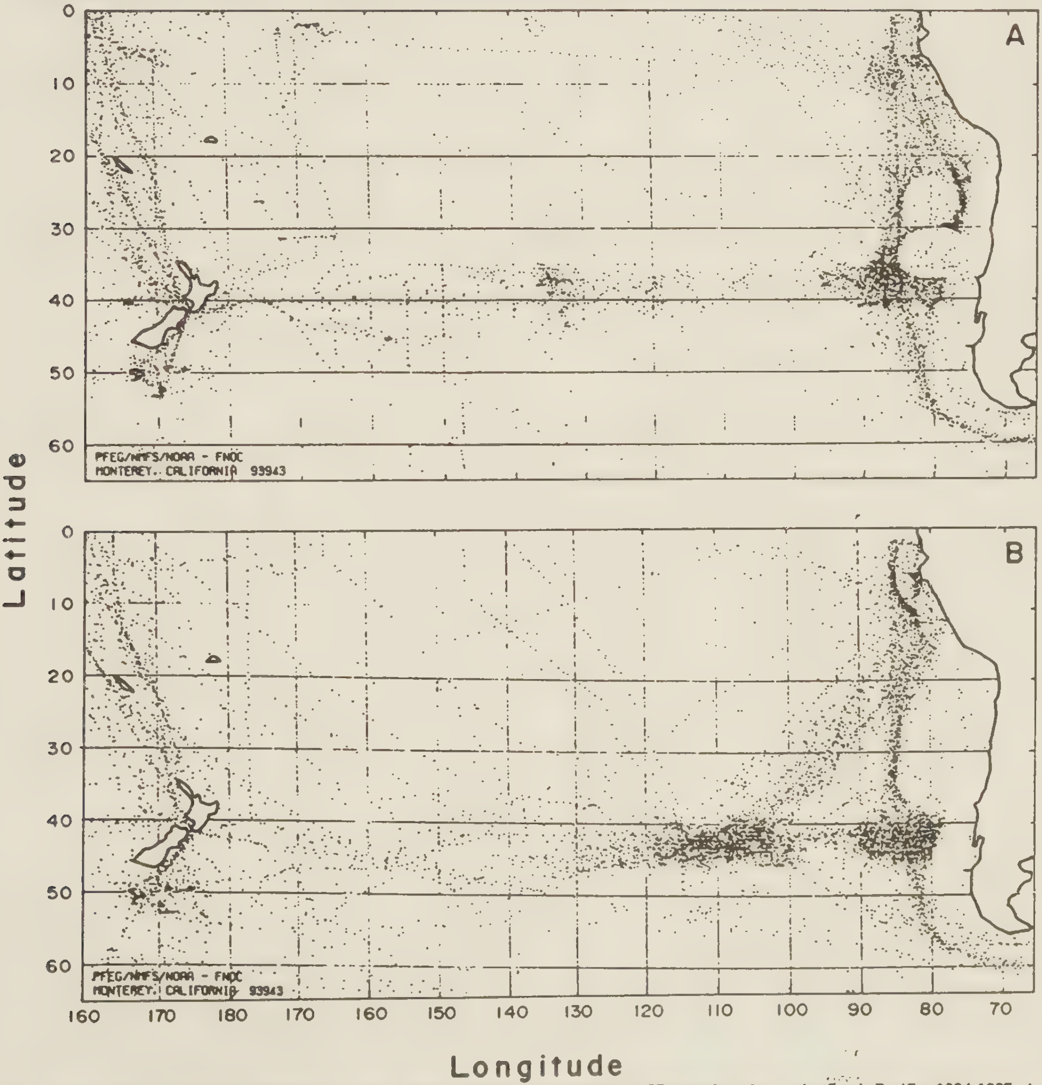

Fig. 3. Seasonal changes in the distribution of ship surface weather observations (USSR vessels only) in the South Pacific, 1984-1987. A. October-December. B. April-June.

Fig. 3. Cambios estacionales en la distribución de las observaciones del clima de los barcos (sólo embarcaciones soviéticas) en el Pacífico Sur, 1984-1987. A. Octubre-Diciembre. B. Abril-Junio.

Review of the Taxonomy of *Trachurus*

As shown above, the recent increase in the world's catch of *Trachurus* is primarily due to increases in the catch off Pacific South America. The FAO catch statistics consider the horse mackerel in this region to be *Trachurus murphyi*, but there is little agreement in the literature as to the correct species name. For example, in Peru the commonly used name is *T. symmetricus murphyi*, whereas in Chile the name *T. murphyi* is used (Santander and Flores 1983; Serra 1983). Therefore a review of the literature on the taxonomy of the horse mackerels was carried out to ascertain the status of the Pacific South American form.

The world's trachurids have been reviewed by Nichols (1920, 1940), Berry and Cohen (1974) and Shaboneyev (1980). Since Nichols (1920) the literature has contained 17 species and 2 subspecies (Table 3). The number and relative size of the scutes along the lateral line and the relative length of the dorsal accessory lateral line has been of primary importance in separating the various forms of *Trachurus* and all three reviews are heavily based on these characteristics. The taxonomy of the group is still in flux and it is not known if the forms in many regions are separate at the species, subspecies or even lower levels. The problem was perhaps best stated by Nichols (1940):

> "The systematic treatment of the forms of *Trachurus* is puzzling. They are sometimes so nearly identical from different oceans that authors synonymize them, but in no case where I have had material for comparison do they seem to me to be quite identical. They might all be races of a single widely distributed species except that two quite unlike forms are often recognized in the same waters."

Nichols (1940) recognized 12 species but he concluded by suggesting that the genus might be divided into 3 species, each having a number of geographically isolated races. Under this arrangement all of the species described to that time would have been races of *T. trachurus*, *T. picturatus* and *T. mediterraneus* (Table 4).

Table 3. Original descriptions of *Trachurus* used in recent literature.
Tabla 3. Descripciones originales de Trachurus *empleadas en la literatura reciente.*

Species	Author(s)	Synonyms
trachurus	Linnaeus 1758	
picturatus	Bowdich 1825	
semispinosus	Nillson 1832	= *trachurus*
declivis	Jenyns 1841	
novaezelandia	Richardson 1843	
japonicus	Temminck and Schlegel 1844	
symmetricus	Ayres 1855	
capensis	Castelnau 1861	
mediterraneus	Steindachner 1868	
murphyi	Nichols 1920	
mucculIochi	Nichols 1920	= *novaezelandia*
lathami	Nichols 1920	
binghami	Nichols 1940	= *lathami*
trecae	Cadenat 1949	
indicus	Nekrasov 1966	
delagoa	Nekrasov 1970	
margaretae	Berry and Cohen 1974	= *delagoa*
Subspecies		
T. mediterraneus ponticus	Aleev 1956	
T. picturatus aleevi	Rytov and Razumovskaya 1984	

Berry and Cohen (1974) synonymized two of the species recognized by Nichols (1940), accepted two new species described by other authors and described a new species; thus recognizing 13 species. They did not group the species as did Nichols but described the relationships between similar forms in different regions. These descriptions result in groups of similar species which are very much like those of Nichols (Table 4). They also showed that there is only one species in the entire western Atlantic *(T. lathami)* and this has recently been verified by Saccardo (1987).

Table 4. Groupings of similar species by various authors.
Tabla 4. Agrupamiento de especies similares según diversos autores.

Nichols (1940)	Berry and Cohen (1974)	Shaboneyev (1980)	No. of [a] scutes	No. of [b] scutes	Scutes[c] depth
Trachurus Races	Similar Forms	*Trachurus* Group			
trachurus	*trachurus*	*t. trachurus*	74.3	72.9	26.4
capensis	*capensis*	*t. capensis*		73.8	
semispinosus		*japonicus*	71.5	71.5	25.6
mucculochi =		= *novaezelandia*	72.4	72.3	22.5
	margaretae[d] (= *delagoa)*	*delagoa*			
Mediterraneus Races	Similar Forms	*Mediterraneus* Group			
		m. ponticus			
mediterraneus	*mediterraneus*	*m. mediterraneus*	83.2	83.3	16.6
lathami	*lathami*	*lathami*	72.5	72.5	12.2
japonicus	*japonicus*		71.5	71.5	
	mucculochi				
	indicus	*indicus*	72.8	74.6	15.5
	trecae[d]	*trecae*	74.3	74.2	13.2
Picturatus Races	Similar Forms	*Picturatus* Group			
picturatus	*picturatus*	*picturatus*	98.3	99.4	13.5
symmetricus	*symmetricus*	*s. symmetricus*	99.0	100.1	17.3
murphyi	*murphyi*	*s. murphyi*	100.3	97.8	17.8
		Aberrant Form			
	declivis[d]	*declivis*	81.6	81.8	23.1

[a] Number of scutes as given in Shaboneyev (1980).

[b] Number of scutes as given by other authors.

[c] Depth of the largest scute in the posterior part of the lateral line as a percentage of head length as given in Shaboneyev (1980).

[d] Berry and Cohen (1974) made no comment on the relationships of these forms.

Shaboneyev (1980) accepted 11 species of *Trachurus*. He followed Nekrasov (1978) and Kompowski (1975) treating *capensis* as a subspecies of *T. trachurus* and he also followed Kotlyar (1976) and Shaboneyev and Kotlyar (1979) in considering *murphyi* to be a subspecies of *T. symmetricus*. Shaboneyev placed the 11 species into three groups of similar species and one aberrant form (Table 4).

The grouping of similar forms by Nichols (1940), Berry and Cohen (1974) and Shaboneyev (1980) are nearly identical and result in a separation of *Trachurus* into a temperate form (the *trachurus* type), a tropical form (the *mediterraneus* type) and an oceanic form (the *picturatus* type). The geographical distributions of Shaboneyev's *trachurus* group (Fig. 4A) and *mediterraneus* group (Fig. 4B) demonstrate the separation into a more temperate group *(trachurus)* and a more tropical group *(mediterraneus)*.

The number of scutes is considerably greater in the oceanic form than the other forms (Table 4) and all three reviews are in agreement in the species included in this group; however, there are minor differences in the inclusion of *japonicus* and *novaezelandia* within the other two groups. These are the two forms which Nichols (1940) was unsure of, stating that *mucculochi* (now *novaezelandia*) should perhaps be included in the *trachurus* group and that *japonicus* should perhaps be included in the *mediterraneus* group. Berry and Cohen (1974) stated that *mucculochi* may be a southern hemisphere cognate of *japonicus* and that *japonicus* was the most morphologically similar to *lathami* and they placed both *mucculochi* and *japonicus* in the *mediterraneus* group. Shaboneyev (1980) separates the various forms in his *trachurus* and *mediterraneus* groups primarily on the relative size of their scutes. In his *trachurus* group the depth of the largest scute in the posterior part of the lateral line averages from 12.2 to 16.6% of the head length; whereas in his *mediterraneus* group it averages from 22.5 to 26.4% (Table 4). He therefore placed both *novaezelandia* (= *mucculochi*) and *japonicus* in his *trachurus* group.

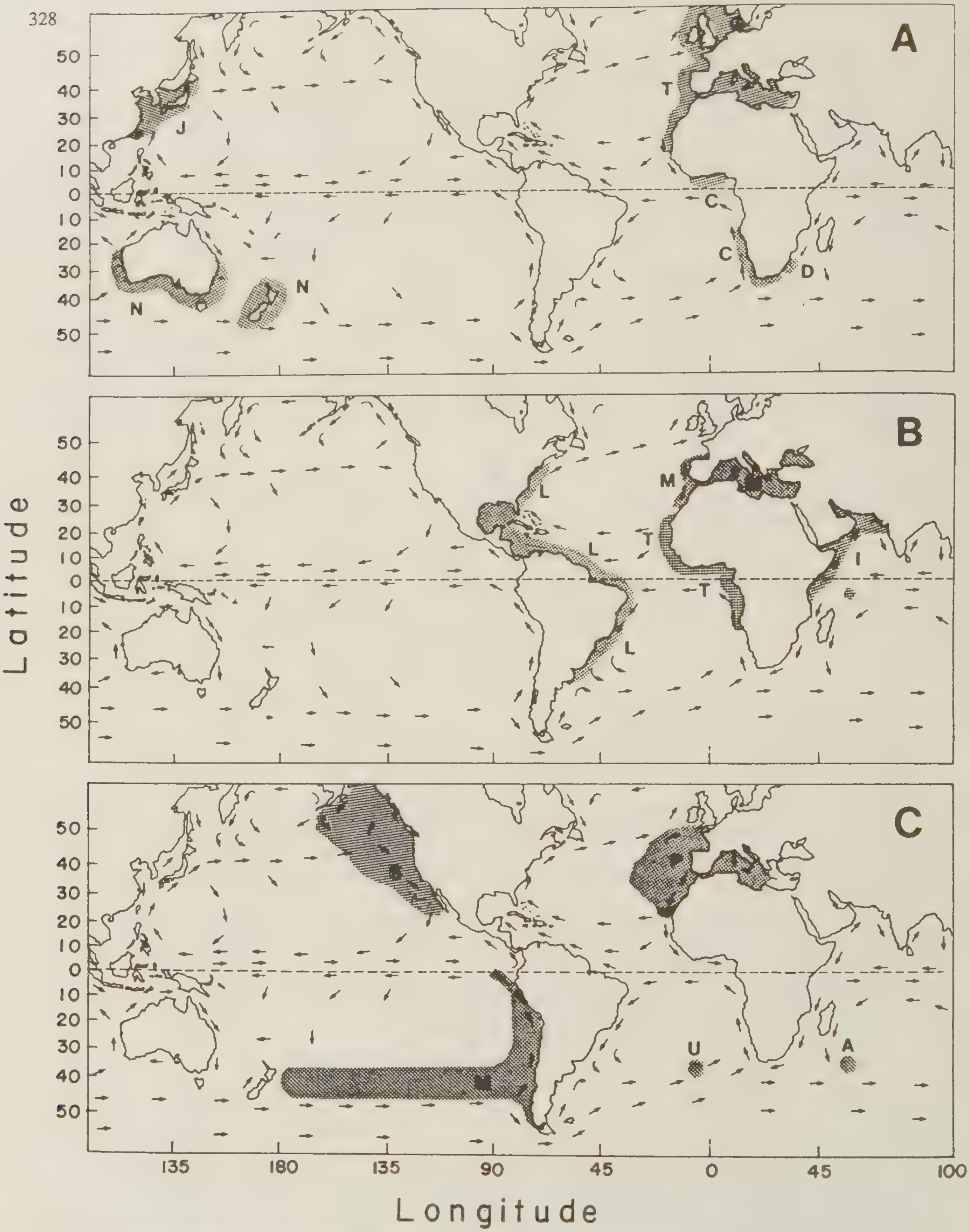

Fig. 4. Geographical distribution of trachurids: A. Shaboneyev's (1980) "*trachurus*" group: *trachurus* (T), *capensis* (C), *novaezelandia* (N), *japonicus* (J) and *delagoa* (D). B. Shaboneyev's (1980) "mediterranean" group: *mediterraneus* (M), *lathami* (L), *trecae* (T), and *indicus* (I). C. Oceanic horse mackerel: *picturatus* (P), *symmetricus* (S), *murphyi* (M), *aleevi* (A) and unnamed (U).

Fig. 4. Distribución mundial de trachuridos: A. Grupo "trachurus" *de Shaboneyev (1980):* trachurus *(T),* capensis *(C),* novaezelandia *(N),* japonicus *(J) y* delagoa *(D). B. Grupo "mediterraneo" de Shaboneyev (1980):* mediterraneus *(M),* lathami *(L),* trecae *(T), y indicus (I). C. Jureles oceánicos:* picturatus *(P),* symmetricus *(S),* murphyi *(M),* aleevi *(A) y sin nombre (U).*

Stephenson and Robertson (1977) showed that *T. muccullochi* was a junior synonym of *T. novaezelandia* and they found no grounds for distinction between *T. novaezelandia* and *T. japonicus*. They did not formally synonymize these forms apparently due to the fact that there is no gene flow across the present day Indo-Pacific gap in their distributions and they felt this necessitated retaining both species. Stephenson and Robertson (1977) also point out the close similarities between *japonicus, novaezelandia* and *lathami*.

There is a general consensus that the members of the *picturatus* or oceanic group are very closely related. Shaboneyev (1980) even states that the members of this group are morphologically so similar that it is difficult to identify them. This consensus rapidly disappears when it comes to deciding whether each is a distinct species or whether they differ at some lower level. Early workers (Jordan and Everman 1896; Meek and Hildebrand 1925) considered them a single species *(T. picturatus)*. Nichols (1940) tried to have it both ways by listing them as separate species but concluded by suggesting that *symmetricus, murphyi* and perhaps *declivis* might stand as races of *T. picturatus*.

Roedel and Fitch (1952) found minor differences between the relative size of scutes in *symmetricus* and *murphyi* but were unable to distinguish *symmetricus* from *picturatus*. Berry and Cohen (1974) gave all three the status of species but considered *murphyi* to be an ecotype of *picturatus* and considered *murphyi* and *symmetricus* to be an antitropical species pair. In contrast, Kotlyar's (1976) extensive morphological analysis of the Peruvian horse mackerel concluded that *murphyi* was not sufficiently different from *symmetricus* to merit species rank and he considered it to be a subspecies *(T.s. murphyi)*.

According to Shaboneyev and Kotlyar (1979), Aleyev (1957) considered the eastern Pacific forms to be a subspecies of *picturatus* and he also considered the northern and southern Atlantic forms of *picturatus* to be separate subspecies. In their morphological analysis of the eastern Pacific forms of *Trachurus* (i.e., *symmetricus* and *murphyi*) and the oceanic horse mackerel *(picturatus)*, Shaboneyev and Kotlyar (1979) state: "our data, based on a considerably greater amount of material, show overlap in all the characters investigated between the oceanic horse mackerel and the eastern Pacific forms of the genus *Trachurus*". However, they found differences in the number of gill rakers which they felt almost reached the subspecies level and differences in the length of the dorsal branch of the lateral line which reached the subspecies level. Although they admitted that they did not find sufficient morphological reasons for considering the eastern Pacific forms and *picturatus* as distinct species, they concluded by suggesting that the ecological differences between them was great enough to merit species rank for the Atlantic and Pacific forms. Their reasons for this conclusion were as follows:

- They considered that *picturatus* differed from the eastern Pacific forms in that it is a neritic-oceanic form widely distributed not only on the continental shelf but also far beyond its boundaries.
- This distribution demonstrated that *picturatus* may live in different water masses, for example, in the cold Canary Current, and in the subtropical waters south of the North Atlantic Current.
- "The most striking contrast with the eastern Pacific forms is provided by the possibility of the existence of the oceanic horse mackerel in the epicontinental Mediterranean, in water masses characterized by heightened salinity."

Recent work has added further complications to the *picturatus* group. Rytov and Razumovskaya (1984) have described a new subspecies of *picturatus (T.p. aleevi)* from the southern Indian Ocean and Evseenko (1987) and Bailey (1989) have shown that *murphyi* occurs in the west wind drift region (along about 40°S) from Chile to New Zealand. According to Rytov and Razumovskaya (1984), "the present grouping of the ocean scads into separate species on the basis of geographic isolation is artificial". They agreed with early authors who recognized only one species of oceanic horse mackerel *(T. picturatus)* which occurs in the eastern North and South Atlantic, the eastern North Pacific, the South Pacific and the southern Indian Ocean.

The distribution of three of the *picturatus* group are presently described; *picturatus* (Shaboneyev and Kotlyar 1979), *symmetricus* (Blunt 1969) and *murphyi* (Serra 1983; and Bailey, in press). Unfortunately the southern Indian Ocean distribution of *aleevi* is not given by Rytov and Razumovskaya (1984), who give only the location of the holotype. The distribution of *picturatus* in the South Atlantic is also poorly documented in the literature and it is further confounded by the fact that *T. picturatus bingami* has been synonymized with *T. lathami* (Berry and Cohen 1974; Saccardo 1987). The only verified record found for *picturatus* from the South Atlantic was the holotype of *Decapterus longimanus*, from Tristan de Cunha examined by Berry and Cohen (1974). The distribution of the *T. picturatus* group as described in the above works is obviously underrepresented in the South Atlantic and Southern Indian Ocean (Fig. 4C). Its occurrence along the warm side of the west wind drift regions of the South Atlantic, South Indian and South Pacific suggests that *picturatus* may occur in a continuous band along the west wind drift region from the South Atlantic to Chile.

As shown above, Shaboneyev and Kotylar's (1979) ecological distinction between the Atlantic and Pacific forms of the *picturatus* group is unwarranted as the eastern Pacific forms should also be considered neritic-oceanic fishes in that they have even more extensive offshore distributions than *picturatus*. They occur from the cold waters of the Gulf of Alaska and Southern Chile to the subtropical waters of Southern Baja California and the Galapagos Islands. They also extend offshore from Chile to New Zealand. It is true that they are not known to occur in waters as saline as the Mediterranean. However, since such waters do not occur in the Pacific Ocean, this does not prove that the eastern Pacific forms are not capable of existing in such water. Therefore, Shaboneyev and Kotylar's (1979) arguments appear to be reduced to the fact that *picturatus* and *symmetricus* differ because they are isolated.

In summary, the differences between the various geographical forms of the oceanic horse mackerel are insuffcent to warrant breaking the group into more than one species. The species *Trachurus picturatus* would appear to have at least three subspecies or races: *T.p. picturatus* in the northeastern Atlantic, *T.p. symmetricus* in the northeastern Pacific and *T.p. murphyi* in the southern ocean. The southern ocean form may be subdivided into three subspecies or races: *murphyi* in the Pacific, *aleevi* in the Indian and an unnamed form in the Atlantic. The recent large increase in the world's catches of horse mackerels therefore comes almost exclusively from exploitation of *Trachurus picturatus murphyi*.

Table. 5. Splitter and lumper classification of the genus *Trachurus*.
Tabla 5. Clasificación desdobladora y englobadora del género Trachurus.

Splitter species (13) and subspecies	Lumper species (7) and subspecies
trachurus	*trachurus*
capensis	*t. trachurus*
novaezelandia	*t. capensis*
japonicus	*novaezelandia*
delagoa	*n. novaezelandia*
mediterraneus	*n. japonicus*
m. mediterraneus	*n. delagoa*
m. ponticus	*mediterraneus*
lathami	*m. mediterraneus*
trecae	*m. ponticus*
indicus	*lathami*
picturatus	*trecae*
p. picturatus	*indicus*
p. aleevi	*picturatus*
symmetricus	*p. picturatus*
murphyi	*p. symmetricus*
declivis	*p. murphyi*
	p. aleevi
	p. unnamed
	declivis

After reviewing the available literature, in my opinion, a definitive analysis of the relationships between the *Trachurus* occurring in different geographical regions cannot be made without a properly designed biochemical genetics analysis. In the absence of such an analysis, the division of the genus into species is probably more a function of the philosophy of individual authors rather than the genetic relationships among the various populations. Therefore, I have included two classification schemes: one for splitters and one for lumpers (Table 5). I also note that considerable further lumping within the *trachurus* and the *mediterraneus* groups may be in order, perhaps even to the three species suggested by Nichols (1940).

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Survey of Fishes and Water Properties of South San Francisco Bay, California, 1973-82

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ABSTRACT

The objective of this study was to describe the physical and ichthyological changes occurring seasonally and annually in the south San Francisco Bay, based on the results of 2,561 otter trawl and water samples obtained between February 1973 and June 1982. Temperature varied predictably among seasons in a pattern that varied little between years. Salinity also underwent predictable seasonal changes but the pattern varied substantially between years. The most abundant species of fish were northern anchovy (*Engraulis mordax*), English sole (*Parophrys vetulus*), and shiner surfperch (*Cymatogaster aggregata*). The majority of the common fish species were most abundant during wet years and least abundant in dry years. Numeric diversity was highest during the spring and early summer, with no detectable interannual trends. Species composition changed extensively between seasons and between years, particularly years with extremely high or extremely low freshwater inflows. All the common species exhibited clustered spatial distributions. Such spatial clustering could affect the interpretation of data from estuarine sampling programs. Gobies (Family Gobiidae) were more abundant during flood tides than during ebb tides. English sole were significantly more abundant in shallower areas. Shiner surfperch showed significant differences in abundance between sample areas.

Introduction

With approximately 3.5 million people living in the area, the San Francisco Bay (also known as the San Francisco Estuary) is heavily impacted by man's activities. One of the most critical environmental issues for this estuary is the role of freshwater inflow. As increasing demands are placed on the freshwater sources to the estuary, it becomes increasingly important to understand the estuary as it is affected by freshwater inflow.

San Francisco Bay has four distinct sections: the delta, north bay, central bay, and the south bay (Fig. 1). The delta is formed by the confluence of the Sacramento and San Joaquin Rivers and is a region of freshwater. The north bay includes the null zone (tidal wedge) which varies in location depending on river outflows (Rozengurt et al. 1987). Most freshwater entering the estuary comes from the delta and passes through the north bay (Conomos 1979). The central bay connects the Pacific Ocean, the north bay, and south bay. Generally quite deep, the cental bay is probably the most diverse region of the estuary based on habitat types, hydrology, and geography. The south bay is shallow, with a mean depth of only 3 meters (McCulloch et al. 1970), and obtains most of its freshwater from the north bay (Conomos 1979). Flushing of the south bay is generally poor.

Two major ecological studies have been conducted on large portions of the San Francisco Bay. One, an ongoing study by the California Department of Fish and Game (DFG), is a long-term sampling program of the entire estuary with the specific goal of determining the effects of freshwater inflow on the estuary. As part of the study, they hope to obtain baseline data and achieve a more complete understanding of the ecology of the estuary (Perry Herrgesell, Calif. Dep. Fish Game, Wilson Way, Stockton, CA 95211, pers. commun. Sept. 1988). To accomplish these goals, DFG samples 42 stations throughout the estuary. Each station is sampled once a month using an otter trawl, a midwater trawl, and a water sampler. They have found that most fish species within the estuary show a mixed response to delta outflows (DFG 1987).

The other important ecological study of San Francisco Bay was done by Aplin (1967), in which he examined six stations in south San Francisco Bay from 1963 to 1966. Each station was sampled once a month using a midwater trawl, an otter trawl, a water sampler, and a sediment sampler. Results were tabulated with little attempt to interpret the data. One of Aplin's sampling stations was located near one of the stations used in the present study, and specific details of his results are compared with those of this study in the ''Species Composition'' section.

This study was undertaken to examine the spatial and temporal variation of selected elements of the fish fauna and of water characteristics of the estuarine habitat in the south San Francisco Bay. By intensively examining a small portion of the estuary from February 1973 to June 1982, it was possible to determine relative abundances by month and year of the most common fish species. Patterns of distribution were also examined. In addition, it was possible to test for the

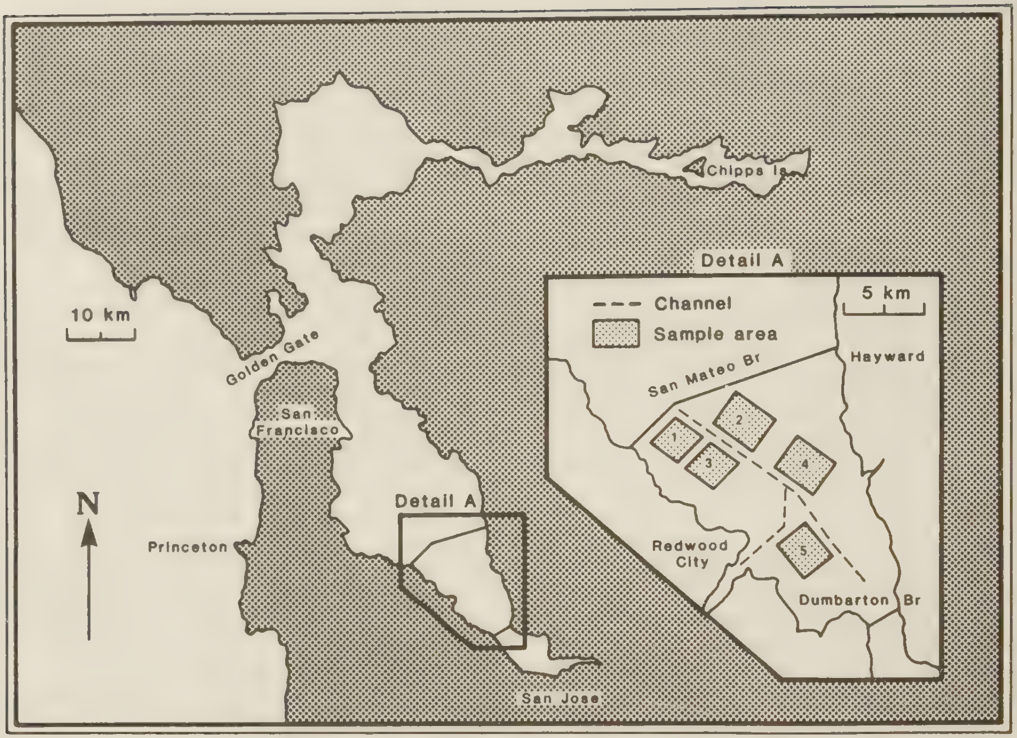

Figure 1
Locations of five sampling stations in south San Francisco Bay, California, used in this study.

effects of tide, time, depth, and location on fish catches. Sampling was done by Marine Ecological Institute (MEI), a private, nonprofit, educational organization, as part of their marine science education program.

This study differs from the Aplin and DFG studies in several respects: its more limited geographic scale, its reliance on a larger number of samples each month (Appendix A) and on longer-term sampling, and the fact that it was conducted as part of an education program. An intensive examination of a small region of the estuary is useful because it reveals some of the small-scale biological characteristics of the environment.

An additional characteristic of this study which makes it valuable is the time-period covered. Two events during the study period, a drought in 1976-77 and two extremely wet years in 1974 and 1980 (Table 1), made it possible to examine the effects of large fluctuations in freshwater inflow on the salinity and biota of the area. The intensive nature of this study allowed reasonably accurate estimates of relative abundances of major species during these events.

Materials and methods

Sampling

During the study period, Marine Ecological Institute (MEI) conducted educational cruises in south San Francisco Bay. Each cruise took four hours, and occasionally two cruises were made in a single day. On a typical cruise, two trawls, two water samples, and a sediment grab sample were made, each at one of five sampling stations (Fig. 1). The time, location, depth, and distance of each trawl were recorded.

The five sampling stations were loosely defined. Each station was bounded on one side by the deepwater channel and on the opposite side by shallows, with roughly defined endpoints. The stations were in depths of 1.5 to 14 meters. Sediment samples were collected with a Petersen grab sampler having a 2-liter capacity or occasionally using a Phleger core sampler with a 1-meter-long shaft. The sediments were qualitatively examined for texture and contents; no attempt was made at quantification. Water samples were collected with a Kemmerer bottle from 1 meter below the surface. The temperature was determined using an electronic meter or occasionally with a thermometer, both with an accuracy of ±0.5°C. Salinity was determined by hydrometer

Table 1

Mean monthly delta outflow values (mean m^3/s) at Chipps Island monitoring station, south San Francisco Bay. Source: Calif. State Water Resour. Board, Sacramento, CA (unpubl. data, Nov. 1988).

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1973	2869	2891	2158	631	331	204	130	169	316	398	1696	2153
1974	3925	1688	2172	3091	723	480	250	362	594	524	679	793
1975	494	1592	1855	977	815	637	315	270	380	478	509	568
1976	265	212	222	250	115	111	123	128	101	103	103	119
1977	124	139	87	87	113	71	91	70	79	59	112	240
1978	1873	1589	2402	1715	1137	257	113	168	334	273	309	249
1979	862	1312	1069	410	380	151	152	98	143	221	345	539
1980	3345	3433	2807	812	592	421	317	118	280	209	189	353
1981	625	618	750	330	254	129	150	90	133	144	1017	2352
1982	2766	2510	2266	3967	1638	807	477	380	734	651	1108	2507
1983	2497	4904	7705	3341	2773	2031	1218	691	887	914	2098	4399
1984	2855	1175	988	417	317	226	289	233	384	337	734	879
1985	428	441	295	196	208	147	139	65	90	267	195	267
Mean	1764	1732	1913	1250	725	436	291	219	343	352	699	1186
SD	1342	1392	1971	1347	759	528	301	176	257	240	629	1287

with an accuracy of ±0.5 ppt. The otter trawl had a 4.9-meter headline, 3.8-cm mesh, with 0.64-cm mesh (stretched) in the codend. The net was secured to the ship with 23-meter warps. After the net was fully deployed, a timer was set for 10 minutes at which time the net was recovered manually. The catch was placed in holding tanks on deck where the fish were counted and identified.

Analysis

Since these data were collected as part of an education program, analysis methods had to take into account several unusual characteristics of the data set. The two most important problems were unequal sampling effort between months and the sometimes imprecise species identifications.

Initially about 3,500 trawls were made. Data were discarded from 939 trawls because of hung-up nets or illegible or misplaced data sheets. A total of 2,561 trawls remained for analysis. To correct for differences in the number of trawls per month (Appendix A), the results were reported as mean catch-per-trawl per month. Statistical techniques capable of handling unequal sample sizes were used as required. All analyses were done on this basis except the species list (Table 2). Data from months with less than five trawls were not used in this study due to the possibility of clustered distributions which might reduce the reliability of abundance estimates.

Based on direct observation and discussion with the ship's crew, some species identifications were considered questionable. In addition, many species had been recorded only to family level. Captured taxa were organized using a simple classification system described below:

Primary species
  1 Readily identifiable to species, and
  2 common (at least 1% of total catch);
Primary family
  1 Readily identifiable to family, and
  2 common (as a family composing at least 1% of catch);
Secondary species
  1 Readily identifiable to species, and
  2 uncommon (<1% of catch);
Secondary family
  1 Readily identifiable to family, and
  2 uncommon (<1% of total catch);
Tertiary species
  1 Identification questionable and/or
  2 uncommon or rare in the catch;
Tertiary family
  1 Identification questionable and/or
  2 uncommon or rare in the catch.

Data on the primary species/families were considered sufficiently reliable to yield valid seasonal and yearly trends and to allow statistical testing of distribution and the effects of trawl variables. The secondary species/family data were deemed inadequate for statistical analysis, and only yearly and seasonal trends were used. Data on the tertiary species/families were considered unreliable, and no analysis was performed.

Seasonal trends were determined from the unweighted mean monthly catch-per-trawl. To determine yearly trends, relative values for the month of peak abundance were compared for each of the primary species/families showing pronounced seasonal trends. Otherwise, the mean monthly catch values were compared over the entire year.

Prior to examining temporal and spatial distribution patterns of the primary species/families, it was necessary to test the effects of tide, time, depth, and location on catches. This was necessary because MEI made no attempt to sample equally at all depths, tide states, times, or sampling stations. In order to combine all of the trawls from an entire

Table 2

Species list for south San Francisco Bay from Marine Ecological Institute's trawl study, 1973-82. (M = marine, F = fresh, E = estuarine, A = anadromous).

Species	Type	*N*	Category
Northern anchovy, *Engraulis mordax*	M	199,389	Primary species
English sole, *Parophrys vetulus*	M	49,469	Primary species
Shiner surfperch, *Cymatogaster aggregata*	M	37,469	Primary species
Gobys, Family Gobiidae		7,017	Primary family
Yellowfin goby, *Acanthogobius flavimanus*	E		
Chameleon goby, *Tridentiger trigonocephalus*	M		
Bay goby, *Lepidogobius lepidus*	M		
Cheekspot goby, *Ilypnus gilberti*	M		
Pacific herring, *Clupea harengus*	M	6,534	Primary species
Sanddabs, Family Bothiidae		6,052	Primary family
Pacific sanddab, *Citharichthys sordidus*	M		
Speckled sanddab, *Citharichthys stigmaeus*	M		
Staghorn sculpin, *Leptocottus armatus*	E	3,344	Primary species
Dwarf surfperch, *Micrometrus minimus*	M	2,446	Primary species
Barred surfperch, *Amphistichus argenteus*	M	1,107	Secondary species
White surfperch, *Phanerodon furcatus*	M	919	Secondary species
Brown rockfish, *Sebastes auriculatus*	M	884	Secondary species
Pile surfperch, *Damalichthys vacca*	M	744	Secondary species
Smelt, Family Osmeridae and Atherinidae		510	Secondary family
Longfin smelt, *Spirinchus thaleichthys*	E		
Surf smelt, *Hypomesus pretiosus*	M		
Night smelt, *Spirinchus starksi*	M		
Topsmelt, *Atherinops affinis*	M		
Jacksmelt, *Atherinopsis californiensis*	M		
California tonguefish, *Symphurus atricauda*	M	507	Secondary species
Brown smoothhound, *Mustelus henlei*	M	461	Secondary species
Leopard shark, *Triakis semifasciata*	M	423	Secondary species
Walleye surfperch, *Hyperprosopon argenteum*	M	388	Secondary species
Bay pipefish, *Syngnathus leptorhynchus*	M	382	Secondary species
White croaker, *Genyonemus lineatus*	M	380	Secondary species
Shad, Family Clupeidae		357	Secondary family
Threadfin shad, *Dorosoma petenense*	F		
American shad, *Alosa sapidissima*	A		
Diamond turbot, *Hypsopsetta guttulata*	M	333	Secondary species
Bat ray, *Myliobatus californica*	M	333	Secondary species
Plainfin midshipman, *Porichthys notatus*	M	310	Secondary species
Bonyhead sculpin, *Artedius notospilotus*	M	265	Secondary species
Starry flounder, *Platichthys stellatus*	E	262	Secondary species
California halibut, *Paralichthys californicus*	M	252	Secondary species
Black surfperch, *Embiotoca jacksoni*	M	123	Tertiary species
Spiny dogfish, *Squalus acanthias*	M	96	Tertiary species
Lingcod, *Ophiodon elongatus*	M	65	Tertiary species
Pacific tomcod, *Microgadus proximus*	M	58	Tertiary species
Pacific sardine, *Sardinops sagax caeruleus*	M	40	Tertiary species
Striped bass, *Morones saxatilis*	A	30	Tertiary species
Sand sole, *Psettichthys melanostictus*	M	22	Tertiary species
Skates, Family Rajidae		14	Tertiary family
Big skate, *Raja binoculata*	M		
California skate, *Raja inornata*	M		
Sturgeon, Family Acipenseridae		9	Tertiary family
Green sturgeon, *Acipenser medirostris*	A		
White sturgeon, *Acipenser transmontanus*	A		
Rubberlip surfperch, *Rhacochilus toxotes*	M	2	Tertiary species
Rainbow surfperch, *Hypsurus caryi*	M	2	Tertiary species
Opaleye, *Girella nigricans*	M	1	Tertiary species
Cabezon, *Scorpaenichthys marmoratus*	M	1	Tertiary species
Rex sole, *Glyptocephalus zachirus*	M	1	Tertiary species
C-O sole, *Pleuronichthys coenosus*	M	1	Tertiary species
Calico rockfish, *Sebastes dallii*	M	1	Tertiary species
Longjaw mudsucker, *Gillichthys mirabilis*	M	1	Tertiary species
Spotfin croaker, *Roncador stearnsii*	M	1	Tertiary species
Saddleback gunnel, *Pholis ornata*	E	1	Tertiary species
Sevengill shark, *Notorynchus maculatus*	M	1	Tertiary species

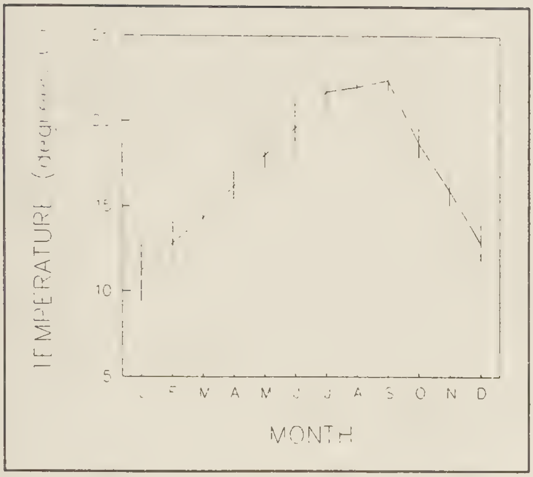

Figure 2
Seasonal temperature trends (mean and standard deviation) in the south San Francisco Bay study area, 1973-82.

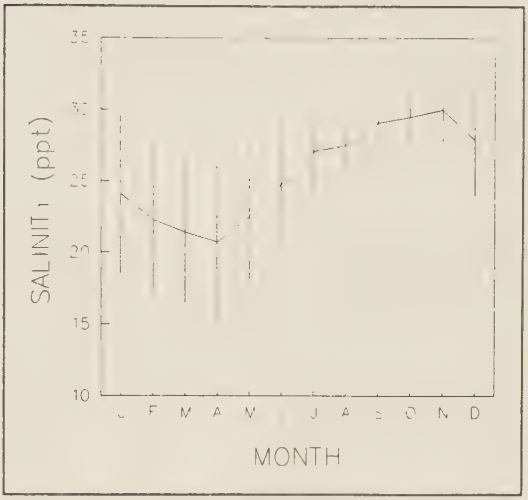

Figure 3
Seasonal salinity trends (mean and standard deviation) in the south San Francisco Bay study area, 1973-82.

month into a single abundance value, it was important to eliminate as many variables as possible. The analysis was also useful for describing the distribution of different species. The 15 months showing highest abundances of the primary species were selected from the data set. A Friedman's test (nonparametric, randomized block design) was employed, with each month used as a block. Those months were omitted in which total catch of a species was less than 5 fish.

To test for the effect of location on catch, the samples were sorted by station, then mean catch-per-trawl was calculated, and the stations were ranked within the block. To test for tidal effects on catch, the trawls from each month were divided into flood- and ebb-tide groups, and mean catch-per-trawl was calculated. To test for the effect of time of day, the samples were sorted into two groups: trawls made before 10:00 a.m., and trawls made after 12:00 p.m. To test for the effect of depth on catch, the samples from each month were divided into two groups: samples from less than 3-meter depths and those taken in depths greater than 4 meters.

To examine distribution patterns, the variance-to-mean ratios for each month were plotted on histograms for each species. The histograms were then inspected for evidence of clustering which would show as skewing of the histogram at some ratio greater than 1.0.

Results

Physical characteristics

Temperature

Water temperatures in the sample area underwent distinct seasonal changes during the study period (Fig. 2). From a mean monthly low in January of 11.0°C, the temperature climbed to a mean monthly high of 22.5°C in September. The highest monthly average was recorded in September of 1979 at 24.5°C, and the lowest mean monthly temperature was in January 1982 at 8.5°C (Appendix B). Standard deviations were less than 1.7°C, indicating little variation from year to year.

Salinity

Salinity also showed a distinct seasonal pattern (Fig. 3), but standard deviations of monthly means between years were high. The mean monthly low of 20.5 ppt (SD = 5.70 ppt) occurred in April. The mean monthly high of 30.0 ppt (SD = 1.7 ppt) occurred in November. The highest monthly salinity was 33.5 ppt in December 1977, and the lowest monthly value was 12.5 ppt in April 1982 (Appendix C). During the 1977 drought, the lowest monthly salinity was 30.5 ppt. Salinity can drop rapidly in the area, as evidenced by a decrease from 30.5 ppt in December 1979 to a mean value of 19.5 ppt in January 1980.

Substrate

Although no quantitative analysis was performed, sediment samples appeared to be similar between stations. The northwest station had a small region of exposed oystershell bed with some live oysters. Otherwise, the substrate consisted of a fine silty clay with variable amounts of crushed shell material. Color of the substrate varied from light brown to dark blackish-brown. Some samples had a strong odor of hydrogen sulfide. Living organisms typically included amphipods, polychete worms, cockles, clams, and mussels. In samples with oyster shells, several other types of invertebrates were observed. Some of the core samples revealed a layer of oyster shells buried at variable depths beneath the top layer of sediment. It was not possible to examine yearly or monthly variations of the substrate samples.

Icthyological characteristics

General

A total of 59 species were observed during the study (Table 2). The species were sorted according to the classification scheme described earlier into six primary species, two primary families, 16 secondary species, two secondary families, 18 tertiary species, and two tertiary families. Of the 59 species, one was a freshwater type, five were anadromous, seven were classified as estuarine, and the rest were marine (Table 2). All of the primary species/families were marine.

Time of day showed no significant effect on the catch of any of the primary species/families (Table 3). Gobies (Family Gobiidae) were significantly more abundant during flood tides than during ebb tides, indicating a movement into the sample areas. English sole (*Parophrys vetulus*) were significantly more abundant in shallower areas. Shiner surfperch (*Cymatogaster aggregata*) abundances were significantly different between stations, with station 4 (Fig. 1) having the smallest catches. These findings made it necessary to assure that each of the significant variables were equally represented in each month. For months when this was not the case, catches of the affected species were sorted, mean catch-per-trawl was calculated for each sort group of the variable, and an unweighted mean catch-per-trawl was computed. These values were then used in subsequent examinations.

The distribution analysis revealed that all of the primary species/families exhibited clustered distributions. Figure 4 shows the histograms of the variance-to-mean ratios for all months in the study. Since all of the histograms show the variance-to-mean ratio is usually much greater than 1.0, there is clear evidence of clustering. Since most species showed no significant differences between stations, the aggregations were considered to be smaller than catches at sampling stations, with the possible exception of shiner surfperch. Of the primary species/families, northern anchovy (*Engraulis mordax*) and English sole exhibited the strongest degree of clustering, and Pacific herring (*Clupea harengus*) and staghorn sculpin (*Leptocottus armatus*) showed the lowest degree. The clustering is probably spatial in nature since there was no difference in catch based on time or tide. The only exception to this was the goby family which are probably both spatially and temporally clustered, with groups of fish moving into the study areas during flood tides.

Seasonal changes

All of the primary species/families except dwarf surfperch show clear seasonal trends (Fig. 5). Although the data are less reliable, the majority of secondary species/families also appear to show pronounced seasonal trends. In nearly all species, peak abundance occurs from March through July with progressively lower abundance through October and November (Appendix D). Some species such as northern anchovy and shiner surfperch were abundant year-round. Others were nearly absent during many months, including English sole which were virtually absent from August through December.

Numeric diversity exhibited a seasonal change, with peak diversity of 5.3 species per trawl occurring in April (Fig. 6). Lowest diversity typically occurred in October, with 2.2 species per trawl. Timing of maximum and minimum diversities varied substantially between years (Appendix E).

Species composition varied substantially among seasons (Fig. 7). While at least six of the eight primary species/families were always among the ten most abundant species, their relative abundances varied substantially through the year. In January the total number of fish was low but relative abundance of the species was fairly uniform. In October the total number of fish was high but relative abundance of the species was decidedly skewed, with two species (northern anchovy and shiner surfperch) making up 95% of the catch.

Table 3

Results of nonparametric randomized block analyses (Friedman's Test) on trawling variables in south San Francisco Bay, 1973-82, from Marine Ecological Institute study. Critical value for depth, tide, and time ($\alpha=0.05$, 1 df) = 3.841. Critical value for location ($\alpha=0.05$, 3 df) = 7.815. Asterisks indicate significant effects.

Species	Depth	Tide	Time	Location
Northern anchovy	0.042	0.657	0.566	1.325
English sole	6.194*	1.887	1.633	3.402
Shiner surfperch	1.887	0.657	0.033	14.960*
Pacific herring	0.657	1.887	3.232	2.805
Goby family	0.657	6.194*	1.633	1.667
Sanddab family	1.887	3.733	1.633	1.111
Staghorn sculpin	3.733	0.042	1.633	0.902
Dwarf surfperch	0.042	0.657	0.566	4.541

Annual changes

Many species exhibited large changes in abundance from year to year (Table 4). Northern anchovy was four times as abundant in 1973 as in any other year. English sole was very abundant in 1974 and nearly absent in 1977. White croaker (*Genyonemus lineatus*) and California tonguefish (*Symphurus atricauda*) were nearly absent in all years except 1977. For those species with identifiable yearly differences, 49% were most abundant in 1974 and 50% were least abundant in 1977. Based on delta outflows (Table 1), 1974 was the wettest year and 1977 was the driest.

Although diversity varied between years, there were no detectable trends in the variation. In a comparison of wet and dry years, both magnitude and timing of high/low diversity appeared to vary randomly (Appendix E). Comparison of the warmest year (1979) with the coldest year (1982) also failed to show any trends.

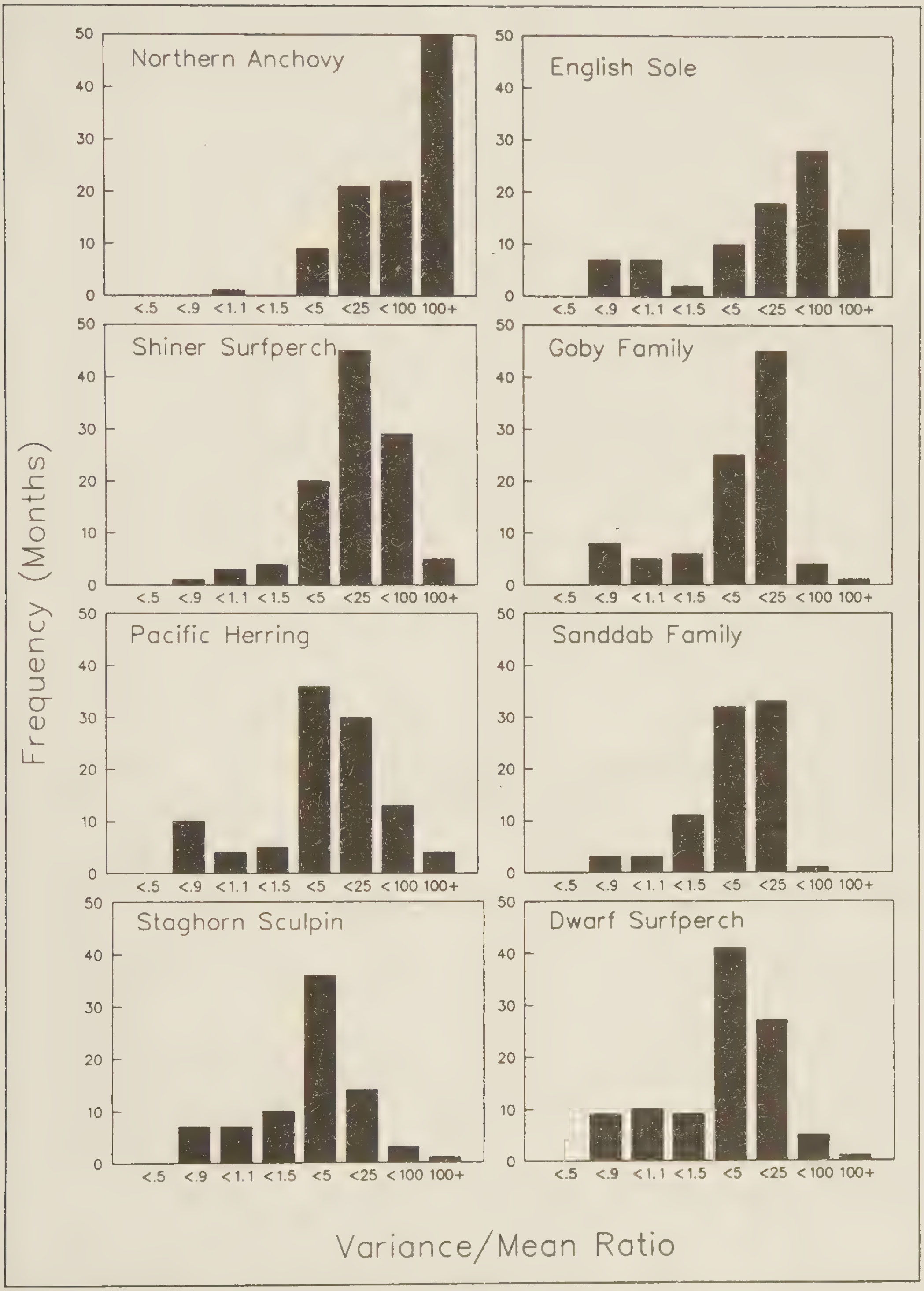

Figure 4

Variance-to-mean ratios of monthly catches of the most abundant fish species collected in otter trawls, south San Francisco Bay, 1973-82. Note the clustered distribution of species in the study area.

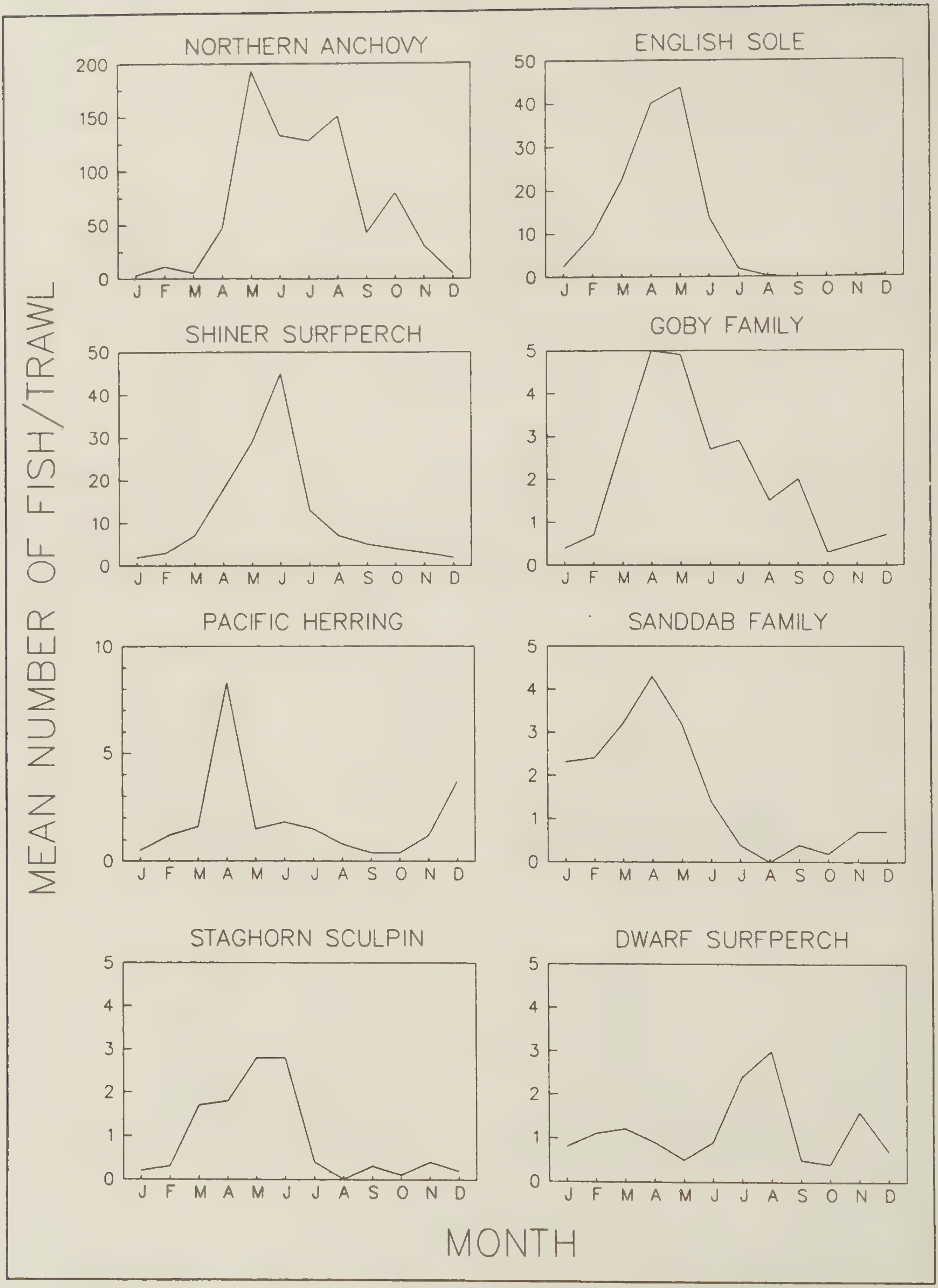

Figure 5
Seasonal abundance trends of the most common fish species caught in otter trawls, south San Francisco Bay, 1973-82.

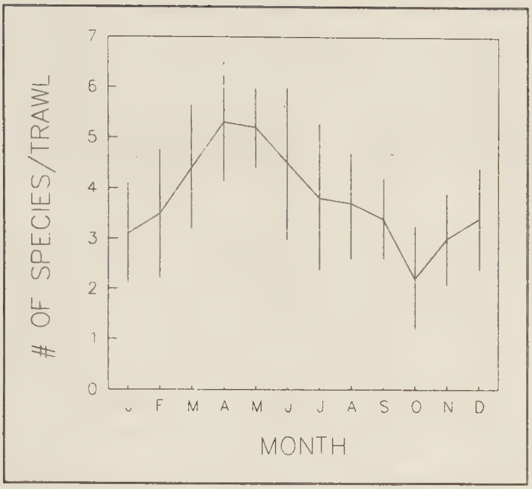

Figure 6
Seasonal trends in numeric diversity of fish species caught in otter trawls, south San Francisco Bay, 1973-82, showing standard deviation range.

Table 4
Highest and lowest abundances of common fish species captured in otter trawls, south San Francisco Bay, 1973-82. Abundances given as mean number of fish per trawl during the month of highest/lowest abundance.

	Highest		Lowest	
Common name	Year	Abundance	Year	Abundance
Northern anchovy	1973	936.8	1980	62.1
English sole	1974	101.2	1977	1.5
Shiner surfperch	1974	85.0	1977	18.2
Goby family	1976	10.2	1978	3.5
Pacific herring	1974	13.9	1977	0.6
Sanddab family	1974	14.0	1976	1.1
Staghorn sculpin	1974	7.4	1977	1.1
Dwarf surfperch	1974	10.8	1977	1.0
Barred surfperch	1979	3.1	1975	0.2
White surfperch	1974	4.5	1977	0.2
Brown rockfish	1974	5.1	1976	0.1
Pile surfperch	1974	4.0	1977	0.1
Smelt family	1977	4.0	?	0.0
California tonguefish	1977	4.7	?	0.0
Brown smoothhound shark	1973	2.8	1979	0.2
Leopard shark	1980	2.3	1977	0.2
Bay pipefish	1979	1.8	1977	0.2
White croaker	1977	7.5	?	0.0
Diamond turbot	1978	1.3	1982	0.1
Bat ray	1976	1.3	1978	0.2
Starry flounder	1974	0.5	1982	0.0

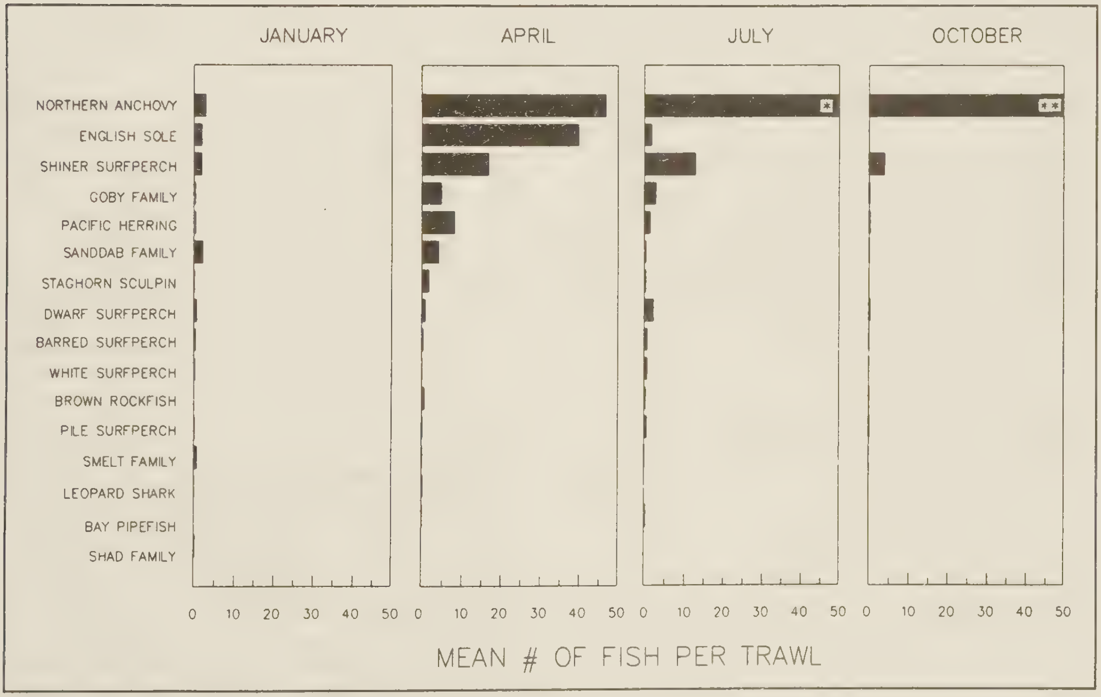

Figure 7
Seasonal comparison of the most abundant species caught in otter trawls, south San Francisco Bay, 1973-82. Abundance values are unweighted. Actual values for northern anchovy exceed the vertical axis (*80 fish per trawl, **129 fish per trawl).

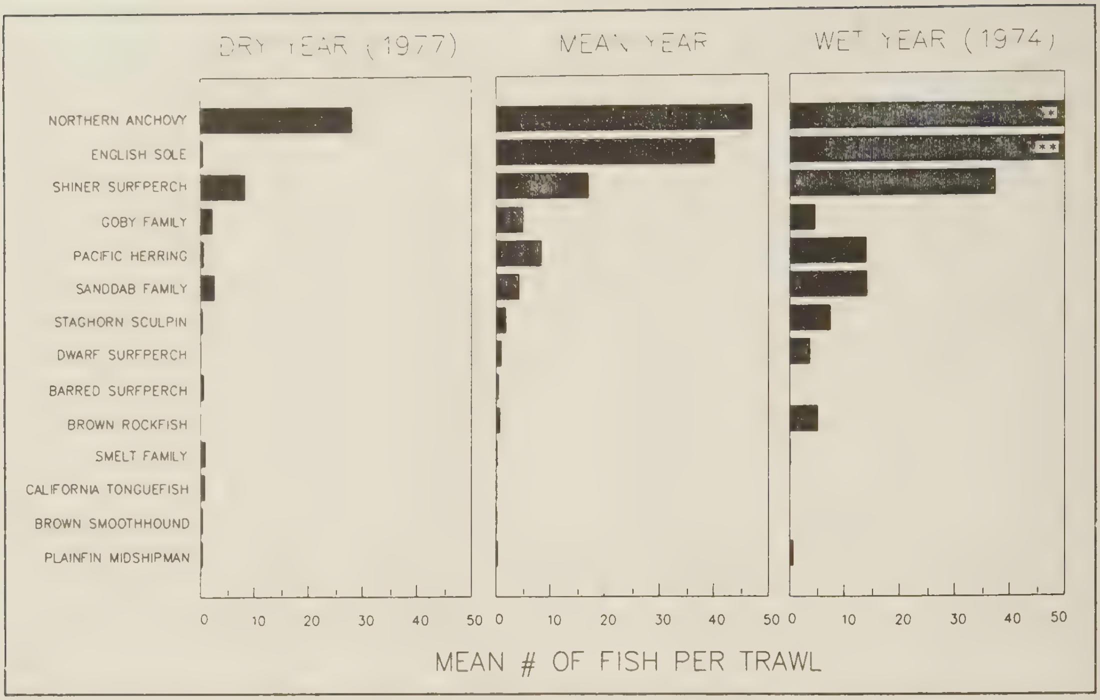

Figure 8

Comparison of species composition in otter trawls, south San Francisco Bay, in April during a wet year (1974), a dry year (1977), and the unweighted mean value for 1973-82. Actual values for northern anchovy and english sole exceed the vertical axis (*61 northern anchovy per trawl, **191 English sole per trawl).

Annual change in species composition was also large (Fig. 8). During the drought year 1977, English sole were effectively absent, many species were present in reduced numbers, and some species were more common. The wettest year, 1974, saw increased abundances of most species but little change in relative abundances of the most common species. This may indicate that excess flows over a certain level may alter only total abundance of species but not species composition, although this is only conjecture.

Discussion

Life history

All of the primary species/families use the estuary as a nursery area, although the estuary may not be the exclusive nursery area for many species (Table 5). Northern anchovy spawn both in the ocean and the estuary and all of its life-cycle stages are found within the estuary. Anchovy were highly abundant throughout their months of spawning (April and September). Although English sole do not spawn in the estuary, juveniles use the estuary for the first year of their life. It is not known how important the estuary is to the survival of juvenile English sole, but one study in Oregon indicates that it may be quite important (Olson and Pratt 1973). Peak abundances of juvenile sole occurred approximately 2-3 months after their peak spawning time in January, which is consistent with the 7-10 week larval stage reported for this species. Shiner surfperch are common both in the estuary and in nearshore coastal waters. In this study shiners were present year-round, although they were most abundant during the spring, when spawning occurs. The gobies (Family Gobiidae) were most abundant during the spring when most species spawn. Pacific herring (*Clupea harrengus*) use the estuary as a spawning ground, laying their eggs on eelgrass beds and hard substrates. Herring support a lucrative fishery within the estuary, although commercial fishing is rare in the sample area. Peak abundance of herring in March coincides with hatching of the eggs in early spring. Sanddabs spawn in the ocean but, like English sole, are found as juveniles within the estuary. Peak abundance of sanddabs in spring does not appear to coincide with any stage in their life cycle. Staghorn sculpin spawn both in the ocean and the estuary during the spring and winter. This may coincide with their late-spring/early-summer peak abundances. Dwarf surfperch spawn both in the estuary and the ocean during late spring and early summer. No clear seasonal trends were

Table 5

Life history stages of selected species collected in south San Francisco Bay as part of Marine Ecological Institute trawl study, 1973-82. Spawning locations: O = ocean, E = estuary, D = delta (or freshwater). Estuarine stages: A = adult, J = juvenile, L = larvae. Lower-case letters imply lesser importance. Source: Wang 1981.

	Spawning		
Species	Location	Months	Stages
Northern anchovy	O/E	IV,IX	A,J,L
English sole	O	XI-II	J,l
Shiner surfperch	E	III-VIII	A,J
Yellowfin goby	O/E	IV-VIII	A,J,L
Bay goby	O/E	XI-VI	A,J,L
Cheekspot goby	O/E	?	A,J,L
Chameleon goby	E	V-VIII	A,J,L
Pacific herring	E	XI-IV	A,J,L
Speckled sanddab	O	III-IX	J,l
Staghorn sculpin	O/E	IX-IV	A,J,L
Dwarf surfperch	O/E	IV-VIII	A,J
Barred surfperch	O/E	?	A
White surfperch	O/E	?	A
Brown rockfish	O	XI-III	J,l
Pile surfperch	O/E	?	A,J
California tonguefish	E	VI-IX	A?,J
Brown smoothhound	O/E		A,J
Leopard shark	O/E	IV-VI	A,J
Walleye surfperch	O/E	III-VIII	A,J
Bay pipefish	E	V-VIII	A,J
White croaker	O/E	XI-V	A,J
Threadfin shad	D	IV-VIII	A
American shad	D	IV-VII	A,J
Diamond turbot	O	III-VII	A,J,l
Bat ray	O/E		A,J
Plainfin midshipman	O/E	V-VIII	A,J,L
Bonyhead sculpin	O/E	?	A,J
Starry flounder	O/E	XI-II	A,J,L
California halibut	O	II-VII	A,J,L

Table 6

Comparison of the ten most abundant species in the south San Francisco Bay, February-July, combined for all years, as reported in this study and in the Aplin study (1967). Species organized according to form used by Marine Ecological Institute.

MEI		Aplin	
Species	%	Species	%
Northern anchovy	61 60	Northern anchovy	95.08
English sole	15.70	Smelt family	2.26
Shiner surfperch	13.70	Shiner surfperch	1.25
Goby family	2.30	Pacific herring	0.77
Pacific herring	1.90	English sole	0.22
Sanddab family	1.80	Shad family	0.19
Staghorn sculpin	1.20	Staghorn sculpin	0.09
Dwarf surfperch	0.90	Goby family	0.07
Barred surfperch	0.40	Striped Bass	0.04
White surfperch	0.30	Leopard shark	0.04

observed for this species, and therefore it is not possible to determine whether a peak exists which would coincide with a stage in their life cycle. Many of the secondary species/families share similar life histories.

Distribution pattern

The majority of species in the study area exhibit spatial clustering on a small scale. Clustering in fish is caused by both behavioral and environmental factors. In the study area there are few distinct habitats: no rocky areas, eelgrass beds, or wharf pilings. The substrate is believed to be relatively uniform. While schooling behavior accounts for the spatial clustering in anchovy, herring, and perch, the explanation for clustering in the flatfish is less clear. It is possible that the benthic environment is less uniform than previously thought. This is supported by the strong contagious distribution of English sole and sanddabs (Fig. 4). Such a distribution could be explained by a variable habitat. Jones (1961) found that benthic invertebrates in the estuary exhibited a clustered distribution. Recent studies by the U.S. Geological Survey (USGS) have found a series of north-south furrows in the south San Francisco Bay (John Chin, USGS, Menlo Park, CA 94025, pers. commun. Oct. 1988). The furrows are hundreds of meters in length, several meters wide, and up to a meter deep. The substrate in the bottom of the furrows may be somewhat coarser than on the sides. The furrows are thought to be hydrological in origin and may account for some of the clustering of benthic fish species. For example, if the bottom of the furrows are found to have substrates more favorable for food, this could cause fish to congregate. This is only speculation, however, and requires further investigation.

Species composition

The most abundant species were found to be northern anchovy, English sole, and shiner surfperch. Aplin (1967) listed northern anchovy, smelts, and shiner surfperch as the most abundant species in the MEI study area. Direct comparison between Aplin's study and ours is not possible, due to Aplin's manner of presentation. However, by computing percent composition for all years during the interval of February-July for each study, it is possible to arrive at a rough comparison of species composition between the two studies (Table 6).

Aplin found large concentrations of northern anchovy, which made up 95% of his catch compared with only 62% of the catch in this study. Smelt (all species combined) made up 2.3% of Aplin's catch but less than 1% of ours. English sole comprised less than 1% of Aplin's catch compared with 16% of ours. Dwarf surfperch were never taken by Aplin, but they were the eighth most abundant species in this study. Aplin collected large numbers of striped bass (*Morone saxatilis*), which were fairly rare in this study. Aplin caught 8 showy snailfish (*Liparis pulchellus*), 2 king salmon (*Oncorhynchus tshawytscha*), and 2 steelhead (*Salmo gairdnerii*), all of which were never caught in our study. During Aplin's 4-year study he recorded 29 species compared with 59 in our 9.5-year study. Explaining these differences provides important insights into the design of a sampling program for the estuary.

The near absence of smelt from this study was in distinct contrast to the high levels in Aplin's study. The DFG study (1987) also indicates large numbers of smelt in the area. The explanation for this difference lies in the fact that the majority of smelt were caught by midwater trawl. The otter trawl is unable to sample the upper water column, and consequently the smelt present in the sample area were not caught in our study. Aplin collected 8 showy snailfish, and the DFG study indicates this species is caught by otter trawl only in the deep channel (Pat Coulston, Calif. Dep. Fish Game, Stockton, CA 95211, pers. commun. Sept. 1988). Since few of the trawls in this study were made in the deep channel, Showy snailfish were missed by MEI. The differences in relative abundance of northern anchovy between the Aplin study and ours can be explained by two factors: use of the midwater trawl, and the patchy distribution of this species. Because Aplin combined the midwater trawls with otter-trawl data, because both otter and midwater trawls can catch large numbers of anchovy, and because there is an overlap in the portion of the water column swept by the two types of net, it is concluded that their abundance in Aplin's study is higher relative to the benthic species than in actuality. The higher abundance of striped bass and the presence of steelhead and salmon are due either to historical changes in abundance or gear effectiveness. In this study, 59 species were collected compared with 29 in the Aplin study. In a study of otter trawls in Santa Monica bay, Fay et al. (1978) concluded that it took more than 100 trawls to catch 95% of the catchable species. Therefore, the difference in number of species may be attributed in part to the small number of trawls used in the Aplin study.

This study examined the effect of location on catch of the primary species/families. Although a significant difference in catch of shiner surfperch was observed between the five stations, the overall effect on the abundance estimates was small; therefore, it can be concluded that a single station can be used to represent a fairly large geographic area. This is an important consideration when designing a sampling program.

Given the clustered distributions found in this study, and the finding by Fay et al. (1978) that multiple tows were required to assess species composition in Santa Monica Bay, it seems apparent that multiple trawls are important for assessing species abundance in a given area. Equally apparent is the necessity for midwater trawls and perhaps other methods (beach seines, gillnets, traps) in analyzing species composition of the estuary.

Wet vs. dry years

Although the primary objective of this study was to examine the ecological nature of the study area, it was also possible to examine the differences between wet and dry years. Although 1982 actually showed higher freshwater inflows than 1980, 1982 was excluded from this comparison because the trawl data were incomplete. Results of this study indicate that the majority of common species were most abundant during wet years and least abundant during dry years (Table 4). The specific objective of the ongoing DFG study is to determine the effect of delta outflows on species abundance within the estuary. A direct comparison between the DFG study and this one is not possible, but an indirect comparison can be made.

DFG has ranked species on a five-step scale based on response to outflow: positive, slightly positive, mixed, slightly negative, and negative. To do this they classified each of the 6 years in their study as either wet or dry and then classified the response of the species. Their study, conducted from 1980 to 1985, included both midwater and otter trawls and was estuary-wide. In order to compare our results with theirs, a similar ranking system was established.

Based on delta outflows (Table 1) 1974 and 1980 were defined as wet years, and 1976 and 1977 as dry years. A species which was most abundant in a wet year and least abundant in a dry year was classified as a positive-response species. If a species was either most abundant in a wet year or least abundant in a dry year, it was classified as a slightly positive-response species. A species with neither highest nor lowest abundance in a wet or dry year, or with both in the same type year, was classified as a mixed-response species. A species with highest abundance in a dry year or lowest abundance in a wet year was classified as a slightly negative-response species. A species most abundant in a dry year and least abundant in a wet year was classified as a negative-response species.

Table 7 compares the observed responses to outflow between our study and the DFG study (1987). Of the species observed in my study, 48% showed a positive response and 10% showed no response compared with 24% and 52%, respectively, in the DFG study. California tonguefish were nearly absent from our study in all years except 1977, when they were very common; thus they were classified as a negative-response species. On the other hand, the DFG study classified them as a positive-response species. English sole, the second most abundant species in this study, were nearly absent during the 1977 drought and were classified as a positive-response species, whereas DFG classified them as a mixed-response species. Pearson (1985) found a significant correlation between delta outflows and English sole abundance in the south San Francisco Bay. The present study indicates that 62% of the species show at least a slightly positive response to wet years. The DFG study indicates 33% of the species showed a slightly positive response or better to wet years.

Table 7

Species abundance responses to increased delta outflows into south San Francisco Bay, as determined by this study and the California Department of Fish and Game study (DFG 1987).

Species	MEI	DFG
Northern anchovy	Slightly negative	Mixed response
English sole	Positive	Mixed response
Shiner surfperch	Positive	Mixed response
Goby family	Slightly negative	Positive
Pacific herring	Positive	Slightly positive
Sanddab family	Positive	Positive
Staghorn sculpin	Positive	Slightly positive
Dwarf perch	Positive	Negative
Barred surfperch	Mixed response	Mixed response
White surfperch	Positive	Mixed response
Brown rockfish	Positive	Mixed response
Pile perch	Positive	Mixed response
California tonguefish	Negative	Positive
Brown smoothhound	Mixed response	Mixed response
Leopard shark	Positive	Positive
Walleye surfperch	Positive	Negative
Bay pipefish	Slightly positive	Negative
White croaker	Negative	Mixed response
Diamond turbot	Slightly negative	Mixed response
Bat ray	Slightly negative	Mixed response
Starry flounder	Slightly positive	Positive

Some of the differences in interpretation between ours and the DFG study may be due to the effect of the different time-periods sampled. In DFG's study, 1981 was classified as dry, but delta outlfows that year were more than twice as great as either year classified as dry (1976 and 1977) (Table 1) in this study. On the other hand, the wettest year in the MEI sampling program (1974) had only about half the volume of delta outflows as the wettest year in the DFG study (1983). Although both studies had extreme ranges of outflows, the effect of the differences between the two studies could be relevant in the interpretation of wet-versus-dry response. In addition, 5 years of the MEI study were not classified as either wet or dry. This conservative approach allows for the possibility of average flows and avoids the forced explanation of species abundance as the effect of either high or low flows. Consequently, it was surprising to find more species showing a strong response (either positive or negative) to outflow in the MEI study than in the DFG study. This is particularly true given that all of the years in the DFG study were classified as either wet or dry.

Geographical variations may also have been responsible for the observed differences. The abundance estimates in the DFG study are based on single monthly trawls in several areas throughout the estuary, while this study used multiple trawls in a small region. The south bay is a distinct and separate part of the estuary. It is possible that when a given species is examined on an estuary-wide basis, as in the DFG study, it will show a different response than when examined on an area-by-area basis. If both the DFG and MEI abundance estimates are accurate, then clearly one possible interpretation is that many species show different responses in different areas of the estuary. In designing a sampling regime for the estuary, two factors are in competition: scope of the study, and sample size. If the scope is limited, the range of questions which can be answered are limited. Typically sample size increases (and therefore reliability) as scope decreases. This study emphasized sample size but was limited in scope. Because of the large sample size used in this study, the estimates of abundance for most species should be reasonably accurate. It would be useful to look for regional differences within species in response to outflows within the estuary when the data become available. It is important, however, to note that this study cannot be applied to the estuary as a whole, but rather only to the southern portion.

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Appendix A
Trawl-effort distribution of Marine Ecological Institute study, south San Francisco Bay, 1973-82.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1973	—	31	22	46	46	22	21	10	1*	35	14	20
1974	20	35	55	36	50	—	—	—	—	12	8	11
1975	3*	—	14	29	41	5	6	—	—	25	23	17
1976	42	56	40	22	55	34	18	—	7	19	29	—
1977	34	14	55	47	58	27	12	—	2*	24	24	7
1978	16	6	22	60	44	36	8	11	—	24	32	—
1979	3*	5	29	37	55	27	19	9	9	22	6	8
1980	8	13	35	31	41	34	13	11	6	4	17	25
1981	20	31	44	60	52	19	12	8	10	19	20	6
1982	6	33	56	58	66	29	—	—	—	—	—	—

Dashes indicate no trawls; asterisks indicate less than 5 trawls (not used in study).

Appendix B
Mean monthly water temperatures (°C) for south San Francisco Bay, 1973-82.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1973	—	13.5	13.0	16.0	19.0	20.0	20.5	21.0	—	18.0	15.0	11.5
1974	10.0	11.5	13.5	16.0	16.5	—	—	—	—	18.0	—	12.5
1975	—	—	13.5	14.0	17.0	21.0	—	—	—	18.5	14.0	11.5
1976	10.5	12.0	15.5	14.5	18.0	17.0	—	—	21.0	19.5	18.5	—
1977	11.0	14.0	13.0	16.5	16.0	18.5	21.0	—	—	18.5	16.0	12.5
1978	13.0	14.0	16.0	17.0	19.0	19.5	21.0	21.0	—	18.5	16.0	—
1979	—	11.0	14.0	16.0	20.0	22.0	23.5	23.0	24.5	20.0	15.5	14.5
1980	13.5	14.0	15.5	18.0	17.5	18.0	22.5	23.0	23.5	19.5	16.5	13.5
1981	12.0	12.5	15.0	17.0	18.5	21.0	21.5	22.0	20.5	17.0	15.5	13.5
1982	8.5	12.5	13.5	16.5	18.0	19.0	—	—	—	—	—	—
Mean	11.2	12.8	14.3	16.2	18.0	19.6	21.7	22.0	22.4	18.7	15.9	12.8
SD	1.8	1.2	1.1	1.2	1.2	1.6	1.1	1.0	1.9	0.9	1.5	1.1

Appendix C
Mean monthly salinities (ppt) for south San Francisco Bay, 1973-82.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1973	—	17.0	18.5	19.0	21.5	23.0	26.0	28.0	—	29.0	26.0	21.0
1974	19.5	16.5	19.5	15.5	18.5	—	—	—	—	28.0	—	27.0
1975	—	—	20.0	18.5	18.0	21.5	23.0	—	—	27.5	28.0	29.0
1976	28.5	28.0	27.5	28.0	29.0	30.0	30.0	—	30.5	30.5	32.0	—
1977	31.0	30.5	30.5	30.5	31.0	32.0	32.0	—	—	33.0	33.0	33.5
1978	24.5	21.0	20.5	18.5	20.0	21.5	25.0	26.5	—	28.0	30.5	—
1979	—	26.0	22.0	22.0	25.0	25.0	27.5	28.5	28.5	30.0	30.5	30.5
1980	19.5	18.0	13.5	18.0	22.5	24.5	25.5	25.5	27.0	28.0	30.0	28.5
1981	29.5	26.5	25.5	24.5	26.0	27.0	28.5	29.0	30.5	31.5	30.0	26.0
1982	16.5	17.5	16.5	12.5	13.5	18.5	—	—	—	—	—	—
Mean	24.1	22.3	21.4	20.7	22.5	24.8	27.1	27.5	29.1	29.5	30.0	27.9
SD	5.7	5.4	5.2	5.6	5.4	4.3	2.8	1.5	1.7	1.9	2.2	3.9

Appendix D

Mean catch-per-trawl of fish species in south San Francisco Bay, 1973-82.

(tr indicates < 1, dash indicates no samples taken)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Northern anchovy												
1973	—	1	1	64	982	357	267	327	—	331	91	5
1974	3	17	27	61	228	—	—	—	—	62	15	10
1975	—	—	tr	40	58	77	145	—	—	61	83	tr
1976	2	tr	3	10	35	155	112	—	24	13	17	—
1977	2	tr	3	28	50	124	72	—	—	26	3	tr
1978	2	2	3	205	200	185	73	226	—	44	37	—
1979	—	71	4	45	89	136	191	159	35	30	9	2
1980	1	7	2	10	62	39	26	31	12	56	5	1
1981	2	8	tr	63	230	88	139	14	100	95	20	14
1982	11	1	3	4	46	34	—	—	—	—	—	—
Mean	3	11	5	47	193	133	128	151	43	80	31	5
SD	3	23	8	59	271	98	76	132	39	98	33	5
English sole												
1973	—	tr	1	11	42	9	3	1	—	0	0	tr
1974	4	17	42	191	108	—	—	—	—	tr	0	tr
1975	—	—	14	48	101	24	9	—	—	tr	tr	1
1976	2	12	9	15	29	17	0	—	0	0	0	—
1977	tr	tr	tr	tr	1	3	0	—	—	0	0	0
1978	8	28	64	29	5	5	tr	tr	—	tr	1	—
1979	—	6	23	30	45	8	0	0	0	tr	tr	tr
1980	tr	5	20	27	63	12	3	0	0	0	0	tr
1981	4	24	47	22	11	4	0	0	0	0	0	1
1982	0	tr	4	22	32	45	—	—	—	—	—	—
Mean	2.4	9.9	22.4	40.1	43.7	13.8	1.9	0.2	0	tr	0.1	0.3
SD	2.8	10.4	21.8	54.6	37.3	13.6	3.2	0.3	0	0.1	0.1	0.4
Shiner surfperch												
1973	—	4	6	20	40	81	37	13	—	7	5	2
1974	2	6	8	37	43	—	—	—	—	2	7	tr
1975	—	—	5	25	44	34	11	—	—	1	tr	tr
1976	tr	2	4	9	34	14	11	—	3	1	tr	—
1977	1	0	5	8	12	20	12	—	—	2	3	2
1978	tr	1	4	15	42	29	2	6	—	4	2	—
1979	—	0	10	7	26	74	6	14	8	2	2	9
1980	tr	tr	12	8	17	50	11	1	3	6	3	4
1981	2	2	4	18	22	29	15	3	7	10	9	0
1982	6	7	14	33	28	36	—	—	—	—	—	—
Mean	2	3	7	18	29	45	13	7	5	4	3	2
SD	2	4	4	11	15	28	10	6	3	3	3	3
Gobies (all species)												
1973	—	0.6	0.5	0.4	1.5	5.8	7.5	2.5	—	0.1	0	0.5
1974	0.3	0.7	1.6	4.6	5.6	—	—	—	—	0.3	1.0	0.5
1975	—	—	2.4	7.8	7.9	0.4	3.3	—	—	0.3	0.2	0.1
1976	0.1	0.1	8.7	10.2	6.4	1.7	3.8	—	6.4	0.1	0.2	—
1977	0.1	0.5	1.1	2.2	4.4	4.2	3.0	—	—	0.3	1.0	0.3
1978	0.3	1.0	1.7	2.1	3.1	3.5	1.8	1.0	—	0.5	0.6	—
1979	—	0.4	1.1	3.2	5.2	1.2	0.5	0.7	0.6	0.1	0	1.0
1980	0	0.2	4.3	5.9	6.0	3.2	2.3	0.5	0.3	0.4	0.1	0.5
1981	1.0	1.5	1.9	4.6	2.6	3.1	1.3	3.0	0.8	0.4	1.2	0.2
1982	0.8	0.7	5.8	9.1	5.9	1.5	—	—	—	—	—	—
Mean	0.4	0.7	2.9	5.0	4.9	2.7	2.9	1.5	2.0	0.3	0.5	0.7
SD	0.4	0.4	2.6	3.2	1.9	1.7	2.1	1.2	2.9	0.2	0.5	0.7

Appendix D (continued)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Pacific herring												
1973	—	1.5	1.1	2.4	1.4	0.2	0.7	0	—	0.3	2.6	15.6
1974	1.3	2.5	8.1	13.9	3.5	—	—	—	—	0	1.9	2.4
1975	—	—	0	0.9	tr	0.1	0.3	—	—	tr	0.7	3.1
1976	1.1	1.3	1.6	9.6	1.5	0.2	0	—	0	0.2	0.1	—
1977	0.1	0.1	0.5	0.6	0.4	0.1	0	—	—	0.2	0.3	1.4
1978	0.1	0.3	0.8	4.5	5.3	0.9	10.3	0.6	—	0.2	0.8	—
1979	—	0.2	0.7	7.1	1.2	3.7	0.1	3.2	0.1	0.1	1.3	1.4
1980	0.6	3.5	1.8	9.7	0.5	0.1	0.9	0.2	1.0	1.4	2.2	1.7
1981	0.2	1.2	0.2	0.5	0.1	0.2	0	0.1	0.4	1.2	0.6	0.2
1982	0.3	0.1	1.0	34.1	1.0	0.1	—	—	—	—	—	—
Mean	0.5	1.2	1.6	8.3	1.5	1.8	1.5	0.8	0.4	0.4	1.2	3.7
SD	0.5	1.2	2.4	10.2	1.7	3.6	3.6	1.4	0.5	0.5	0.9	5.3
Sanddabs (all species)												
1973	—	2.5	4.4	4.4	4.2	0.3	0.4	0.1	—	0	0.1	0.2
1974	1.8	4.2	4.2	14.0	12.1	—	—	—	—	0.1	0	0.2
1975	—	—	0.6	tr	1.4	0.8	0	—	—	0	tr	0.4
1976	0.4	0.5	0.4	0.8	0.4	1.1	0.1	—	0.6	0.1	tr	—
1977	0.8	0.7	2.3	2.6	3.2	6.6	1.6	—	—	0.5	1.4	1.1
1978	6.6	2.5	6.8	6.4	1.6	0.1	0	0	—	0.7	1.0	—
1979	—	2.6	5.5	5.4	4.5	0.2	0	0	0	0	0.7	1.9
1980	2.7	1.8	1.5	3.0	1.7	2.1	0.8	0	0	0	0.3	1.2
1981	1.9	3.6	1.8	1.8	1.4	0.6	0.1	0	0.9	0.5	2.5	0
1982	1.7	3.7	4.9	4.4	1.1	1.2	—	—	—	—	—	—
Mean	2.3	2.4	3.2	4.3	3.2	1.4	0.4	tr	0.4	0.2	0.7	0.7
SD	2.1	1.3	2.2	3.9	3.4	2.0	0.5	tr	0.5	0.3	0.9	0.7
Staghorn sculpin												
1973	—	0.5	4.4	2.1	3.6	15.9	0.9	0.1	—	0	0.1	0.2
1974	0.1	0.8	1.7	7.4	6.8	—	—	—	—	0.1	0	0.1
1975	—	—	0.7	2.2	3.2	1.8	0.3	—	—	0.1	0.1	0.4
1976	0.2	tr	0.3	0.7	4.0	1.6	0.7	—	1.0	0.1	0.1	—
1977	0.2	0	0.4	0.4	0.4	1.1	1.0	—	—	0.3	2.3	0.3
1978	0.3	0.8	1.8	0.8	0.6	0.4	0	0	—	0	tr	—
1979	—	0	3.6	1.6	3.1	1.9	0.1	0	0	0	0	0
1980	0.1	0.1	1.1	1.7	3.5	1.0	0.3	0	0	0	0.4	0.4
1981	0.2	0.4	2.9	0.8	1.1	1.2	0	0	0.2	0.2	0.2	0
1982	0.3	0.5	0.4	0.8	1.4	0.6	—	—	—	—	—	—
Mean	0.2	0.3	1.7	1.8	2.8	2.8	0.4	tr	0.3	0.1	0.4	0.2
SD	0.1	0.3	1.4	2.0	2.0	4.9	0.3	tr	0.5	0.4	0.6	0.2
Dwarf surfperch												
1973	—	1.5	0.8	1.8	2.3	1.4	10.8	10.0	—	0.4	0.4	0.6
1974	4.4	2.2	4.5	3.7	0.9	—	—	—	—	0.9	5.1	0.1
1975	—	—	0.9	0.1	0.2	0	1.3	—	—	0.1	0.1	0.2
1976	0	0.1	0.2	0.3	0.1	0.1	0.3	—	0.1	0	tr	—
1977	0.7	0.1	0.3	0.1	0.1	0.3	1.0	—	—	0.2	1.0	0.4
1978	0.1	0.2	1.4	0.3	0.2	0.3	0.4	1.0	—	0.9	0.3	—
1979	—	0	1.0	0.7	0.1	0.9	3.0	3.1	0.7	0.1	4.8	3.1
1980	0	0	0.5	0.1	0.2	tr	0.7	0.5	0.3	0.6	0.5	tr
1981	0.7	1.3	0.8	0.9	0.2	4.4	1.8	0.4	0.8	0.2	2.4	0.5
1982	0	4.6	1.6	0.5	0.1	0.3	—	—	—	—	—	—
Mean	0.8	1.1	1.2	0.9	0.5	0.9	2.4	3.0	0.5	0.4	1.6	0.7
SD	1.6	1.5	1.3	1.1	0.7	1.4	3.5	4.1	0.3	0.3	2.0	1.1

Appendix D (continued)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Barred surfperch												
1973	—	0.1	0.3	0.2	0.2	1.5	2.0	0.3	—	0.1	0.1	0.2
1974	0.1	0.2	1.7	1.3	0.1	—	—	—	—	0	0.3	0.2
1975	—	—	0	0.1	0	0.2	0	—	—	0.9	1.0	1.2
1976	0.8	0.6	tr	0	0.1	0	1.0	—	0	0	0	—
1977	0	0.3	tr	0.6	1.3	0.1	2.3	—	—	0	0.1	0.1
1978	0.8	0.8	2.1	0.3	0.3	0.5	0.3	0	—	tr	0.2	—
1979	—	0.3	0.2	0.1	1.0	3.1	0.2	0	0	0	0	0.5
1980	0.7	1.2	0.1	0.1	0.1	tr	0.4	0	0.7	0.6	0.2	0.2
1981	0	0.8	0.3	0.6	0.2	0.3	0.1	0.8	0.3	0.6	0.1	2.7
1982	1.2	0.5	0.3	0.3	0.5	0.6	—	—	—	—	—	—
Mean	0.5	0.5	0.5	0.4	0.4	0.7	0.8	0.2	0.2	0.2	0.2	0.7
SD	0.5	0.4	0.7	0.4	0.5	1.0	1.0	0.3	0.3	0.3	0.3	0.9
White surfperch												
1973	—	0	0	tr	0.1	4.0	4.6	0	—	0.3	0.1	0.1
1974	1.0	0.3	4.5	0.1	0.3	—	—	—	—	0	0	0
1975	—	—	0.1	0.7	0	0.4	0	—	—	0	0	0
1976	0.6	0	0	0	0	0	1.0	—	0	0	0	—
1977	0.2	0	0	0	0	0.2	0.1	—	—	0.1	0.4	0
1978	0	0	0.1	0.1	2.8	1.0	0	0	—	0.1	0	—
1979	—	0	0.1	0	0.1	0	0	0.1	0	0	1.0	0
1980	0	0	0.1	0	0	0.3	0	0	0	0	0	4.3
1981	0	0.1	0.1	0	0.1	0.1	0	0	0.1	0.1	0	0.2
1982	0	0.1	0	0	0	0	—	—	—	—	—	—
Mean	0.3	0.1	0.5	0.1	0.3	0.6	0.8	tr	tr	0.1	0.2	0.7
SD	0.4	0.1	1.4	0.2	0.9	1.2	1.7	tr	tr	0.1	0.3	1.6
Brown rockfish												
1973	—	0	0	0.1	0.2	0.8	1.1	0.2	—	tr	0	0.1
1974	0.5	0.7	1.4	5.1	1.2	—	—	—	—	0	0.1	0
1975	—	—	0	0.2	0.1	0	0	—	—	0	0	0.1
1976	tr	0	0	0.1	tr	0	0.1	—	0.1	0	0	—
1977	0	0	0	0	0	0.8	1.2	—	—	0.1	0.1	0
1978	0	0	0.3	tr	0.1	0.6	0	0.2	—	0.7	0.2	—
1979	—	0	1.4	0.3	0.3	0.1	0.1	0.2	0	0	0	0.8
1980	0	0	tr	0.3	tr	tr	0.2	0	1.3	0.2	0.1	0.8
1981	0.1	0.2	0.4	0.3	0.2	1.5	0.8	0.4	0.8	0.3	1.2	0.3
1982	0.3	0.2	0.7	0.4	0.4	0.3	—	—	—	—	—	—
Mean	0.1	0.1	0.4	0.7	0.3	0.5	0.4	0.2	0.6	0.2	0.2	0.3
SD	0.2	0.2	0.6	1.6	0.4	0.5	0.5	0.1	0.6	0.2	0.4	0.4
Pile surfperch												
1973	—	0.7	0.1	0.3	0.5	0.4	2.4	4.0	—	1.5	0.6	1.1
1974	1.4	0.8	0.9	0.7	0.1	—	—	—	—	1.5	1.4	0.6
1975	—	—	0.1	0	0.3	3.6	0	—	—	0	0.4	0
1976	0	0	0	0	0.1	0.4	0.2	—	0.3	0	0	—
1977	0.1	0.1	0.1	0	0	0.1	0	—	—	0	0.5	0.1
1978	0.1	0	0.1	0.1	0.3	1.6	0	0.3	—	0	0.2	—
1979	—	0.2	0.3	0.6	0.1	0.3	0.3	0.4	0.1	0	0.3	0.6
1980	0	0	0	0.1	0	0.1	1.5	0	0.2	0	0	0
1981	0.1	0.1	0.1	0.1	0	1.2	1.5	0	0	0.1	0.1	0.2
1982	0	0.2	0.1	0	0	0.4	—	—	—	—	—	—
Mean	0.2	0.2	0.2	0.2	0.1	0.9	0.7	0.9	0.2	0.3	0.8	0.4
SD	0.5	0.3	0.3	0.3	0.2	1.1	1.1	1.7	0.1	0.7	0.9	0.4

Appendix D (continued)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Smelts (all species)												
1973	—	0.3	0.1	0.2	0	0	0.1	0	—	0.1	0.3	0.2
1974	0.4	0.1	0.2	0.1	0.2	—	—	—	—	0	0	0
1975	—	—	0	0.3	0.6	0	0	—	—	0	0	0
1976	0.2	0.3	0	0.3	0	0	0.1	—	0	0.2	0	—
1977	4.0	3.0	0.7	0.9	0.1	0	0	—	—	0	0.1	0.4
1978	0.4	0	0.1	0.1	0	0	0	0	—	0	0	—
1979	—	0.8	0.2	0.1	0	0	0.1	0	0.1	0.1	0	0.1
1980	0.1	0.2	0.3	0.1	0	0	0.1	0	0	0	0	0.1
1981	0.2	0.1	0	0.1	0	0	0	0	0	0	0.2	0
1982	0	0.1	0.2	0.1	0.2	0	—	—	—	—	—	—
Mean	0.8	0.5	0.2	0.2	0.1	0	0.1	0	tr	tr	0.1	0.1
SD	1.4	1.0	0.2	0.2	0.2	0	0.1	0	tr	0.1	0.1	0.1
California tonguefish												
1973	—	0	0	0	0	0	0.1	0	—	0	0	0
1974	0	0	0	0	0	—	—	—	—	0	0	0
1975	—	—	0	0	0	0	0	—	—	0	0	0
1976	0	0	0	0	0	0	0	—	0	0	0	—
1977	0	0	0.2	0.8	3.4	4.7	2.8	—	—	0	0	0
1978	0	0	0	0	0.2	0.3	0	0.1	—	0	0	—
1979	—	0	0	0	0	0.1	0.1	0	0	0	0	0
1980	0	0	0	0.1	0.3	0.3	0.3	0.2	0.2	0	0	0
1981	0	0	0	0	0	0	0.1	0	0	0	0	0
1982	0	0	0	0	0.1	0.1	—	—	—	—	—	—
Mean	0	0	tr	0.1	0.4	0.6	0.4	0.1	0.1	0	0	0
SD	0	0	tr	0.3	1.1	1.5	1.0	0.1	0.1	0	0	0
Brown smoothhound sharks												
1973	—	tr	0	tr	0.6	2.8	0.3	0	—	0.1	0.1	0.1
1974	0	tr	tr	0	0.3	—	—	—	—	0.1	tr	0.1
1975	—	—	0	0.1	0.6	0.2	0	—	—	0.1	tr	0.1
1976	0	0.1	0	0	0.4	0.7	0.1	—	0.1	0	tr	—
1977	0	0.1	0.1	0.4	0.7	0.9	0.2	—	—	0.3	0.4	0.6
1978	0.1	0	0	tr	0.2	0.2	0.1	0	—	tr	0.2	—
1979	—	0	0.1	0.1	0.2	tr	0	0.1	0.1	0.1	0	0.3
1980	0	0.1	0	0.1	0.4	0.9	0	0	0	0	0.3	0.1
1981	0.1	0	0	0.2	0.2	0.1	0.1	0.1	0.2	0.3	0	0
1982	0	0	0	tr	0	0	—	—	—	—	—	—
Mean	tr	tr	tr	0.1	0.4	0.6	0.1	0.1	0.1	0.1	0.1	0.1
SD	tr	tr	tr	0.1	0.2	0.9	0.1	0.1	0.1	0.1	0.2	0.2
Leopard sharks												
1973	—	tr	0	0.3	0.8	2.3	0	0	—	tr	0	0
1974	0.1	0.2	0.1	0.2	0.2	—	—	—	—	0.2	0.5	0.1
1975	—	—	0	0.3	0.1	0	0	—	—	0	tr	0.2
1976	0.1	0.1	0.2	0.2	0.2	tr	0	—	0	0	0	—
1977	0	0.1	0.1	0.4	0.7	0.9	0	—	—	tr	0.1	0.1
1978	0.1	0.2	0.2	0.2	0.5	0.1	0	0.1	—	0	tr	—
1979	—	0	1.0	0.1	tr	0	0.1	0	0.2	0	0	0.5
1980	0.3	0	0	0.8	0.2	0.4	0	0.2	0	0	0.2	tr
1981	0.2	0.1	tr	0.5	tr	0	0	0	0	0	tr	0
1982	0	0.1	0.3	0.1	0.1	0	—	—	—	—	—	—
Mean	0.1	0.1	0.2	0.3	0.2	1.2	tr	0.1	0.1	tr	0.1	0.1
SD	0.1	0.1	0.3	0.2	0.2	2.7	tr	0.1	0.1	1.0	0.2	0.2

Appendix D (continued)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Walleye surfperch												
1973	—	0	0	0	0.2	0.3	0.1	0	—	tr	0	0
1974	0	0.3	tr	0	tr	—	—	—	—	0	0	0
1975	—	—	0	0.1	0.1	0	0	—	—	0	0	0
1976	0	0	0	0	0	tr	0.2	—	0	0	0	—
1977	0	0	0	0	0.1	0.2	0.3	—	—	0	0	0
1978	0	0	0	0	0.1	2.8	0	1.1	—	0	0	—
1979	—	0	0.1	0	tr	0.4	0.2	0.9	0	0	0.3	0.8
1980	0	0	0.1	0	0.1	1.4	0	0	0	0	0	0.1
1981	0.3	tr	0.1	0.1	tr	0.7	0	0.1	0.1	0.1	0.2	0
1982	0.3	0	tr	0.1	0.3	2.3	—	—	—	—	—	—
Mean	0.1	tr	tr	tr	0.1	0.8	0.1	0.4	tr	tr	0.1	0.1
SD	0.1	0.1	0.1	tr	0.1	0.9	0.1	0.5	0.1	tr	0.1	0.3
Bay pipefish												
1973	—	0.1	0	tr	0.1	0.1	2.6	0.3	—	tr	0.1	0
1974	0	0.1	0.2	0.5	0.6	—	—	—	—	0.1	0.1	0
1975	—	—	0.1	0	0.1	0	0	—	—	0.2	tr	0
1976	0	0	0.2	0.9	tr	tr	0.1	—	0.4	0	0.1	—
1977	0	0.1	0	tr	0	0	0.2	—	—	0	tr	0
1978	0	0	0.1	0.1	0.7	0.1	0.1	0.2	—	0.2	0.1	—
1979	—	0	tr	0.1	0.2	0.2	0.4	0.7	1.8	0.4	0	0
1980	0	0.2	0.1	0.3	0.4	0.4	0	0.2	0.7	0.1	0.2	0.1
1981	0.1	0.1	0.1	tr	tr	0.1	0.2	1.1	0	0.1	0	0
1982	0.2	0	tr	0	0	0	—	—	—	—	—	—
Mean	tr	0.1	0.1	0.2	0.2	0.1	0.4	0.5	1.5	0.1	0.1	tr
SD	0.1	0.1	0.1	0.3	0.3	0.1	1.0	0.4	1.2	0.1	0.1	tr
White croaker												
1973	—	0	0	0	0	0	0	0	—	0	0	0
1974	0.1	0	0	0	0	—	—	—	—	0	0	0
1975	—	—	0	0	0.1	0	0	—	—	0	0	0
1976	0	0	0	0	0.1	0	0	—	0	0	0	—
1977	0	0	0.1	0.3	1.5	7.5	0	—	—	0	0	0
1978	0	0	0.1	0	0	0	0	0	—	0	0	—
1979	—	0	0.1	0	0	0	0	0	0	0	0	0
1980	0	0	0	0	0	0.3	0	0	0	0	0	0
1981	0	0	0.1	0.2	0	0	0	0	0	0	0	0
1982	0.2	0	0.1	0.1	0.2	0	—	—	—	—	—	—
Mean	tr	0	0.1	0.1	0.2	0.9	0	0	0	0	0	0
SD	0.1	0	0.1	0.1	0.5	2.5	0	0	0	0	0	0
Shad (all species)												
1973	—	0.2	0	0.1	0	2.7	0.1	0	—	0	1.2	1.5
1974	1.2	0.5	0	0	0	—	—	—	—	0	0.4	1.1
1975	—	—	0.2	0.1	0	0	0	—	—	0	0.4	0.8
1976	0.6	0.9	0.3	0.1	0	0	0.2	—	0	0	0	—
1977	0	0	0	0	0	0	0	—	—	0	0.8	0.6
1978	0.4	0.2	0.1	0	0	0	0	0	—	0	0.1	—
1979	—	0.6	0.2	0.1	0	0	0	0	0	0	0	0
1980	0	0.5	0	0	0	0	0	0	0	0	0	0.4
1981	0.1	0	0	0	0	0	0	0	0	0	0.1	0.3
1982	0	0	0	0	0	0	—	—	—	—	—	—
Mean	0.3	0.3	0.1	tr	0	0.3	tr	0	0	0	0.3	0.7
SD	0.4	0.3	0.1	tr	0	0.9	tr	0.1	0	0	0.4	0.5

Appendix D (continued)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Diamond turbot												
1973	—	0.1	0.4	0.1	0.1	1.3	0.2	0	—	0	0	0.2
1974	0	0.2	0.2	0.2	0.1	—	—	—	—	0.1	0	0.2
1975	—	—	0	0.2	0.2	0	0	—	—	0	0	0.1
1976	0.2	tr	0.1	0.2	tr	0	0	—	0.1	0	0	—
1977	0.1	0	0.1	0.2	0.1	0.2	2.5	—	—	tr	0.8	0.9
1978	0.5	1.3	0.3	0.2	0.2	0	0	0	—	0	0	—
1979	—	0	0.1	0.2	tr	0	0	0	0	0	0	0.1
1980	0	0	0.7	0.2	0.1	0.1	0	0.1	0	0	0	0
1981	0.1	0.1	0.1	0.1	tr	0	0	0	0.5	0	0.1	0
1982	0	tr	0.1	0.1	0.1	0	—	—	—	—	—	—
Mean	0.1	0.2	0.2	0.2	0.1	0.2	0.3	tr	0.2	tr	0.1	0.2
SD	0.2	0.4	0.2	0.1	0.1	0.4	0.8	tr	0.2	tr	0.3	0.3
Bat rays												
1973	—	0	0	tr	0.4	1.3	0.2	0.1	—	tr	0.1	0
1974	0	0	0.1	0.3	0.3	—	—	—	—	0.1	0.3	0
1975	—	—	0.1	0.1	0.2	0	0	—	—	0	tr	0
1976	0	tr	0.2	0.6	0.2	0.3	0.1	—	0	0	tr	—
1977	0	0.1	0.1	0.3	0.3	0.3	0.3	—	—	0.2	0.1	0
1978	0	0	0.1	tr	0.2	0.1	0	0	—	0	0.1	0
1979	—	0.2	tr	0.2	0.4	0	0.1	0.2	0.4	0	0	0
1980	0	0.1	tr	tr	0.3	0.4	0	0	0	0	0.2	0
1981	0	tr	0.2	0.6	tr	0	0	0.1	0.3	0.3	0.2	0
1982	0	0	0	0	tr	tr	0.3	—	—	—	—	—
Mean	0	0.1	0.1	0.2	0.2	0.3	0.1	0.1	0.2	0.1	0.1	0
SD	0	0.1	0.1	0.2	0.1	0.4	0.1	0.1	0.2	0.1	0.1	0
Plainfin midshipmen												
1973	—	0	0	0.2	0	0.1	0.2	0.2	—	0	0	0
1974	0	0	0.1	0.6	0	—	—	—	—	0	0	0
1975	—	—	0	1.1	0.4	0.2	0	—	—	0	0	0
1976	0	0	0	0	0.1	0	0.4	—	0.7	0	0	—
1977	0	0	0	0.4	0.3	0.2	0	—	—	0	0	0
1978	0	0	0	0.1	0.1	0	0	0	—	0.1	0.3	—
1979	—	0	0.2	0.2	0	0	0.3	0.4	0	0	0	0
1980	0	0	0.1	0.2	0	0.2	0.2	0.2	0.2	0.2	0.1	0.2
1981	0	0	0	0.1	0	0	0	0	0	0	0.2	0
1982	0	0	0.1	0.5	0.3	0	—	—	—	—	—	—
Mean	0	0	0.2	0.3	0.1	0.1	0.1	0.2	0.2	0	0.1	0
SD	0	0	0.1	0.2	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1
Bonyhead sculpin												
1973	—	0	0	0	0	0	0	0	—	0	0	0
1974	0	0.1	0.2	1.0	0.1	—	—	—	—	0.1	0	0.3
1975	—	—	0.1	tr	0.1	0.2	0	—	—	0	0	0
1976	0	tr	0	0	tr	0	0	—	0	0	0	—
1977	0	0.2	0.2	0.2	0.2	tr	0	—	—	0	0.2	0
1978	0.1	1.3	0.1	0.1	0.2	0.2	0	0	—	0	tr	—
1979	—	0.2	tr	0.1	0	tr	0.1	0	0	0	0	0.3
1980	0	0.2	0.4	0.2	0.1	0.2	0.2	0	0	0	0.1	0
1981	0.4	0.2	0.5	0.1	0.1	0.1	0.3	0	0	0	0	0.2
1982	0.2	0.2	0.3	tr	0.1	0.1	—	—	—	—	—	—
Mean	0.1	0.3	0.2	0.2	0.1	0.1	0.1	0	0	tr	tr	0.1
SD	0.1	0.4	0.2	0.3	0.1	0.1	0.1	0	0	tr	0.1	0.1

Appendix D (continued)

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Starry flounder												
1973	—	0.5	0.5	0.2	0.2	0.1	0.1	0	—	0	0	0.2
1974	0.4	0.2	0.1	0.1	0.1	—	—	—	—	0.1	0.3	0.2
1975	—	—	3.7	0.6	0.1	0	0.3	—	—	0	0.1	0.2
1976	0.1	0.1	tr	0.1	tr	tr	0	—	0	0	tr	—
1977	0	0	tr	0.1	tr	tr	0	—	—	0	0.3	0.1
1978	0.3	0.2	0	tr	0.2	0	0	0	—	tr	0.1	—
1979	—	0	tr	0.1	0	0	0	0	0.1	0	0	0
1980	0	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.5	0.2	0.1	0.1
1981	0.3	0.1	0.3	tr	tr	0	0.1	0	0	0	0	0
1982	0	0	tr	0	tr	0	—	—	—	—	—	—
Mean	0.1	0.1	0.5	0.1	0.1	tr	0.2	tr	0.2	tr	0.1	0.1
SD	0.2	0.1	1.1	0.2	0.1	tr	0.2	tr	0.2	0.1	0.1	0.1
California halibut												
1973	—	0	0.3	0.1	tr	0	0	0.2	—	tr	0	0
1974	0	tr	0.1	0.1	0	—	—	—	—	0	0	0.9
1975	—	—	0.1	0.1	0	0	0.3	—	—	0	0	0.1
1976	0.1	0.5	0	0	0	0	0	—	0	0	0	—
1977	tr	0.2	tr	tr	tr	0	0.1	—	—	0	0.4	1.1
1978	0.9	1.8	0.6	0.1	0.1	0	0	0.2	—	0.7	0.5	—
1979	—	0.2	0.5	0.8	0.4	0.1	0	0	0	0	0	0
1980	0	0.2	tr	0	0	tr	0	0	0	0	0.1	tr
1981	0	0.1	0.1	tr	tr	0	0	0.1	0.1	0.1	0.2	0
1982	0	0.2	0.1	0.1	0.1	tr	—	—	—	—	—	—
Mean	0.1	0.4	0.1	0.1	0.1	tr	0.1	0.1	tr	0.1	0.1	0.3
SD	0.3	0.6	0.2	0.2	0.1	tr	0.1	0.1	0.1	0.2	0.2	0.5

Appendix E

Mean number of species per otter trawl in south San Francisco Bay, 1973-82. Dash indicates no trawls.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1973	—	2.8	4.4	5.8	6.6	5.0	6.2	5.3	—	2.6	3.1	3.1
1974	4.4	4.8	5.8	8.3	6.2	—	—	—	—	3.1	3.5	3.1
1975	—	—	3.0	4.6	5.5	4.8	2.2	—	—	1.8	1.7	3.1
1976	2.4	1.8	2.8	4.7	4.5	4.0	2.9	—	3.7	1.5	1.3	—
1977	1.9	1.4	3.2	4.2	4.9	5.8	5.3	—	2.0	2.8	4.1	3.9
1978	3.8	5.3	5.3	4.1	5.2	4.9	2.5	3.5	—	3.2	2.8	—
1979	—	3.8	6.2	6.0	5.2	3.7	3.0	4.4	3.2	1.8	3.8	5.4
1980	2.4	3.8	3.9	4.7	4.8	5.4	4.3	2.5	3.7	2.4	3.2	2.6
1981	2.7	3.9	4.0	4.8	3.6	5.1	3.6	3.0	4.2	3.4	4.0	2.3
1982	4.0	4.0	5.2	5.3	5.3	5.0	—	—	—	—	—	—
Mean	3.1	3.5	4.4	5.3	5.2	4.5	3.8	3.7	3.4	2.2	3.0	3.4
SD	1.0	1.3	1.2	1.2	0.8	1.5	1.4	1.1	0.8	1.0	0.9	1.0

8953

PERRIN, E.V.D., K. BENIRSCHKE, W.F. PERRIN.

Wayne State University. Detroit, Michigan. University of California. San Diego, California. NOAA. La Jolla, California

MONSTROUS DOLPHINS - Malformations in Marine Mammals.

Most reproductive failures in aquatic creatures are lost to study, unless the animals thrive in captivity. The base incidence of malformations therefore is unknown and the discovery of unusual anomalies may or may not be significant. In the Southwest Fisheries Center of NOAA collection of dolphin embryos, fetuses and adults obtained from inadvertent kills on tuna boats, we have obtained several most unusual specimens: (1) Severe caudal regression; (2) Megalencephaly; (3) Omphalocele; (4) Cleft mandible and hypoplasia of maxilla; (5) Monozygotic twins. These are well-described in the literature of teratology in land mammals. Caudal regression syndrome is known to be associated with maternal diabetes mellitus, megalencephaly with a variety of metabolic disorders as well as an isolated finding. Cleft mandible with midfacial hyoplasia, omphalocele and identical twins are apparently chance events. Considering the state of contamination of the oceans, and knowing that these dolphins all were taken from the same general area in the tropical Pacific, it may be possible in furture to link these findings with some xenobiotic contaminants. The role of delayed implantation in the production of monozygotic twinning has to be clarified.

8954

Annex H
Report of the Sub-Committee on Small Cetaceans

Members: Amos, Anganuzzi, Aurioles, Balcomb, Bannister, Best, Bjørge, Broadhead, Brownell, Buckland, Cawthorn, Collet, da Silva, DeMaster, Goodall, Hall, Hammond, Heyning, Holt (R.), Holt (S.), Hoelzel, Horwood, Inagaki, Jones, Joyce, Kasuya, Kato, Leatherwood, Lens, Lockyer, Martin, Mate, Mead, Misaki, Miyashita, Moore, Morimoto, Nakamura (T.), Pallsbøl, Perrin (Convenor), Pitman, Puddicombe, Reilly, Sanpera, Scott (G.), Scott (M.), Smith, Swartz, Vidal, Vikingsson, Whitehead.

1. ELECTION OF CHAIRMAN

Perrin was elected Chairman.

2. APPOINTMENT OF RAPPORTEURS

Balcomb, Heyning and Mead acted as rapporteurs for the sessions on beaked whales. Buckland, Reilly, Collet and G. Scott also served as rapporteurs.

3. ADOPTION OF AGENDA

The Agenda adopted is given in Appendix 1.

4. REVIEW OF AVAILABLE DOCUMENTS AND REPORTS

The sub-committee considered documents SC/40/SM1–23 and the national progress reports. SC/40/O 9–13, 15, 16, 21, 22, 28–31, 37–39 and SC/40/Mi18 also contained information on small cetaceans.

5. REVIEW OF POPULATION BIOLOGY AND EXPLOITATION OF BEAKED WHALES, ZIPHIIDAE

5.1 Berardius bairdii

5.1.1 Distribution and stock identity

The overall distribution of Baird's beaked whale is limited to the North Pacific Ocean and adjacent seas. Kasuya (SC/40/SM8) reported on the distribution of Baird's beaked whales in the western North Pacific, Sea of Japan and the Sea of Okhotsk as determined from whale sighting cruises made during 1982–1987. Each of these areas is probably inhabited by a separate stock or population, as the whales occur concurrently in summer and autumn months along the Pacific coast of Japan (Jun-Sep: Omura *et al.*, 1955; SC/40/SM8), in the Sea of Japan (Jun-Aug: Omura *et al.*, 1955; Oct: Nishimura, 1970) and near ice floes in Soviet waters of the Okhotsk Sea (April/May, Dec: Fedoseev, 1985). The whales are not known to transit the relatively shallow straits between the regions or to enter the East China Sea (Yang, 1976; Zhou, 1986). The Pacific coast stock probably inhabits continental slope waters between the fronts of the Kuroshio and Oyashio Currents, north of about 34°N. The mid-winter distribution of the putative stocks is unknown.

There is no recent information available about Baird's beaked whales around the Kurile Islands, but Sleptsov (1955) reported the species from the Kamchatka Peninsula and the western Bering Sea along the ice edge as far north as Cape Navarin (65°N) in summer months. Strandings have been reported from the Commander Islands and St. Matthew Island in the Bering Sea as well as the Aleutian Islands and Siberia (SC/40/SM21). The whales from this region may represent yet another stock or population.

The eastern North Pacific stock (or stocks) of this species occurs in summer and autumn from Alaska (SC/40/SM21) and Vancouver Island to as far south as the tip of Baja California (23°N) (SC/40/SM13; SC/40/SM14).

Ohsumi (1983) mapped the distribution of Baird's beaked whales across the mid–latitudes of the entire North Pacific Ocean (with notable densities near the Emperor Seamount Chain and north of Hawaii) from sightings reports of Japanese whale scouting ships. However, accuracy of the identifications has been called into question and there is no way to confirm them. Kasuya reported that the Japan Fisheries Agency will send four vessels to the North Pacific for two months this summer (1988), to survey for all marine mammals between 3°N and 45°N across the entire ocean from Japan to North America. The sub–committee looks forward to seeing the report of these surveys, to resolve, in part, whether Baird's beaked whales are in fact distributed in oceanic waters far offshore.

The distributional evidence to date indicates that *Berardius bairdii* is a cold-water deep-diving species that has good potential for separate stocks and populations in the regions mentioned. Amos and Hoelzel noted that if so, recently developed molecular methods may shed light on stock identity.

5.1.2 Abundance

Miyashita (1985) calculated an abundance estimate of 4,220 for the western North Pacific population of Baird's beaked whale from sightings data. The CPUE data do not show a clear annual trend from 1947 to 1983 (SC/36/SM14), so it is not known if the population is diminishing or stable. Kasuya noted that in addition to the expanded general surveys for marine mammals mentioned in 5.1.1, there will be another vessel conducting dedicated surveys for Baird's beaked whales and pilot whales in Japanese coastal waters this summer (1988). The sub-committee looks forward to receiving the results of those surveys at its next meeting, to re-examine population size of the western North Pacific stock. There are insufficient data available for any of the other putative stocks to allow estimation of abundance.

5.1.3 Migration

SC/40/SM8 stated that the results of sightings cruises made during 1982–87 supported the conclusions of Omura *et al.* (1955) that Baird's beaked whales leave the Pacific coast of Japan in winter months. The Sea of Japan stock may possibly remain isolated there during all seasons. The Okhotsk Sea stock apparently inhabits waters near Hokkaido in late spring and fall and retreats to the north during the summer months. Its winter distribution is unknown, but Kasuya noted that some of these whales may migrate to the east of the Kuril Islands in winter when the southern Okhotsk Sea is filled with ice. As noted by Fedoseev (1985), others may remain in small open leads in the northwestern Okhotsk Sea in winter months. Dohl (1983) reported from aerial surveys along the California coast that Baird's beaked whales were present along the continental slope in summer and fall but absent in winter, a seasonal pattern which is similar to that found in the western Pacific.

5.1.4 Life history

SC/40/SM7 reported on the biological examinations of 135 Baird's beaked whales taken in 1975 and 1985–1987 in a fishery on the Pacific coast of Japan. As Omura *et al.* (1955) and Nishiwaki and Oguro (1971) had noted, the catches are primarily of sexually mature males. From examination of layers in the tooth cementum, it was determined that males attain sexual maturity at 6–10 GLGs (growth layer groups – Perrin and Myrick, 1980) at a length of about 9.1 to 9.7m, and females attain sexual maturity at 10–14 GLGs at a length of 9.8 to 10.6m. One GLG likely equals one year (Kasuya, 1977). The sex ratio of juvenile whales in the catch is approximately 1:1, but for whales with over 20 GLGs it is strongly biased toward males. There does not seem to be obvious differential catchability of males and females that could explain this imbalance in catch, although it could be due to behavioural factors, such as adult males swimming peripherally in the school. The oldest female had 54 GLGs and the oldest male 84, with a correspondingly unusual age distribution suggesting a significantly higher mortality rate in females. The sub-committee discussed the significance of a higher female mortality rate for this species and was unable to explain it, while noting that SC/40/SM22 reported a similar situation in *Ziphius cavirostris* from stranded specimens. Aurioles (1987) reported a similar distribution in a mass stranding of seven Baird's beaked whales near La Paz, B.C., Mexico. The annual pregnancy rate for adult females has been estimated at 0.30, and the ovulation rate at 0.47.

Prey items include benthic fishes (Moridae and Macrouridae) and cephalopods (Omura *et al.*, 1955; Nishiwaki and Oguro, 1971; and SC/40/SM16), which indicates deep-water feeding in the western Pacific. Rice (1963) reported macrourid fish from *B. bairdii* taken off central California. The diet of these whales in the shallow waters of the northwest Okhotsk Sea is not known. Baird's beaked whales are heavily parasitised internally in the stomach, liver, blubber and kidney with extensive tissue pathology noted in the latter due to the nematode *Crassicauda giliakiana* (SC/40/SM15).

5.1.5 Exploitation

See Table 1 for Japanese catches. Small numbers were also taken at various land stations along the US and Canadian coast in the eastern Pacific.

Table 1

Catches of Baird's beaked whales by small-type whaling off Japan (*Rep. int. Whal. Commn* 33: 633 and ProgReps Japan)

Year	Catch	Year	Catch	Year	Catch	Year	Catch
1948	76	1958	229	1968	117	1978	36
1949	95	1959	186	1969	138	1979	28
1950	197	1960	147	1970	113	1980	31
1951	242	1961	133	1971	118	1981	39
1952	322	1962	145	1972	86	1982	60
1953	270	1963	160	1973	32	1983	37
1954	230	1964	189	1974	32	1984	38
1955	258	1965	172	1975	46	1985	40
1956	297	1966	171	1976	13	1986	40
1957	186	1967	107	1977	44	1987	40

5.1.6 Status

The CPUE data for the Western Pacific do not show a clear annual trend from 1947 to 1983 (SC/36/SM14), so it is not known if that population is diminishing or stable. The Government of Japan sets an annual national quota on the harvest of this species of 40. The whaling industry has divided this into 35 in the western Pacific and 5 in the Okhotsk Sea.

5.2 Berardius arnuxii

5.2.1 Distribution and stock identity

Joyce reported on sightings of Arnoux's beaked whales during IDCR cruises in Antarctic waters from 1978/9–1987/8. This species was seen in Antarctic Areas II, IV, V and VI, but it was noted that in earlier cruises some sightings may have been simply logged as 'unidentified ziphiid' or not logged at all. Balcomb noted that he had plotted sightings in Southern Hemisphere waters from logbook entries of Japanese whale scouting ships before 1975 (kindly provided by Ohsumi); but, as with the sightings data for the species' North Pacific congener, there may be some question as to the accuracy of some of the identifications. Goodall and SC/40/SM23 provided data on strandings of Arnoux's beaked whale from all southern continents, noting that they have tended to cluster around New Zealand (perhaps reflecting effort). The conclusion from sightings and strandings is that the species is circumpolar in distribution, occurring throughout the Southern Hemisphere in cool temperate, sub-Antarctic and Antarctic waters. The northernmost stranding was at 34°S in South Africa, and the southernmost was at 64°S on the Antarctic Peninsula (Godoy and Goodall, pers. comm.). Sightings of these whales have been made very near the ice edge and amongst ice floes in the Antarctic pack. Some have been known to become entrapped in pack ice (Taylor, 1957).

The largest male reported was 960cm long and the largest female of confirmed length 885cm. Both were mature and smaller than typical specimens of mature *B. bairdii* (SC/40/SM23). It has been suggested that this species is conspecific with *B. bairdii* (McLachlan *et al.*, 1966; Ross, 1984).

5.2.2 Abundance

Nothing is known about the absolute abundance of Arnoux's beaked whales, but Kasamatsu *et al.* (1988) noted that they are significantly less common than southern bottlenose whales (*Hyperoodon planifrons*).

5.2.3 Migration

Nothing is known about migration.

5.2.4 Life history

Nothing is known about the life history of Arnoux's beaked whales. Kasamatsu *et al.* (1988) and Balcomb reported that the species is often gregarious and has been seen in groups numbering up to about 80 individuals. There was a mass stranding of four animals in Hawke's Bay, New Zealand. According to SC/40/SM23, most strandings have been in summer. The life history of this species is presumably similar to that of *B. bairdii*, taking into account its smaller size (Mead, 1984).

5.2.5 Exploitation

Arnoux's beaked whales are not presently commercially taken in any directed fisheries, nor have they ever been taken in any significant numbers (Brownell, 1974).

5.2.6 Status

No information.

5.3 Hyperoodon ampullatus

Unless otherwise referenced, the information below for *Hyperoodon* spp. is abstracted from Mead (in press).

5.3.1 Distribution

Northern bottlenose whales are distributed in the North Atlantic from Nova Scotia to about 70°N in Davis Strait, along the east coast of Greenland to 77°N and from England to the west coast of Spitzbergen. There is a single record from the White Sea. In the North Sea, strandings have been reported from Belgium, Denmark, France and England. There are a few records from the Mediterranean. In the western Atlantic, there are two main centres of distribution, one in the area called 'The Gully' just north of Sable Island, Nova Scotia and the other in Davis Strait off northern Labrador. Strandings have been reported from as far south as Rhode Island. This is a deep-water animal, usually inhabiting waters more than 2,000m deep.

Sightings from the North Atlantic are presented in SC/40/O 9, 11, 15 and 29.

5.3.2 Abundance

A recent line-transect survey yielded preliminary estimates of 3,142 bottlenose whales off Iceland and 287 off the Faroe Islands (SC/40/O 30). Vikingsson reported that allowance was not made in the survey for animals missed due to long dives.

5.3.3 Migration

There is evidence from the distribution of catches that a northward migration occurs in the eastern Atlantic in April-July. The southward migration begins in July and continues to September.

5.3.4 Life history

Length at birth is about 350cm. Asymptotic length in males of about 850–900cm is reached at about 20 GLGs and in females of about 750cm at about 12 GLGs. One GLG is assumed to correspond to one year in this species. Fifty-three females from Labrador ranged in age from 1 to 50 GLGs; 75 males ranged from 1 to 37 GLGs. Modal age in adults was 12 GLGs for females and 16 for males. Maximum recorded age is 27 (?) GLGs for females and 37 for males.

Minimum lengths of sexually mature animals (n=5,224) were 600cm for females and 730cm for males. Mean length at attainment of sexual maturity was 690cm in females and 750cm in males. Minimum age at sexual maturation has been estimated at 7 GLGs in both sexes, with the average at 11 GLGs in females and 7–11 GLGs in males. Average mature testis weight is about 600g; the maximum recorded was 2,600g for both testes combined.

Gestation is estimated at 12 months. Lactation is estimated to last at least one year. The mean calving interval is estimated to be two years. The largest recorded foetus was 360cm long and the smallest calf 350cm. Calving takes place in the spring.

The bottlenose whale feeds on deep-living squids and fishes; an extensive list of taxa recorded from stomach contents is given in Mead (in press).

5.3.5 Exploitation

The Norwegian fishery can be divided into two periods: 1882 to 1920s, and 1930s to 1973. The catches during the first period have been estimated at 72,000. When the modern period began, a government licence was required, and more exact records were kept; a total of 5,043 whales were taken during the period 1938–1969. The fishery closed in 1973 when only 3 whales were caught. The peak annual catch during the modern period was 700. A small fishery operated out of Nova Scotia and took 87 whales in 'The Gully' during the period 1962–67.

5.3.6 Status

The minimum initial population has been estimated at about 28,000. The consensus is that the aggregate North Atlantic population is depleted, but there is disagreement about the degree of depletion (Holt, 1977). The stock(s) were classified as a provisional Protected Stock in 1977. The species is currently classified as 'Vulnerable' by the IUCN.

5.4 Hyperoodon planifrons

5.4.1 Distribution

The southern bottlenose whale has a wider distribution than that of *H. ampullatus*; it occurs in the entire Southern Ocean and north to about 30° S. It is possible that some sighting records involve misidentifications, as it is difficult for non-experts to distinguish between this species and *Berardius arnuxii*. R. Best *et al.* (1986) recently reported a sighting in November of 5 animals which they referred to the species at 5°42'S and 34°1'W (off northeast Brazil). Due to the extremely low latitude of this sighting, particularly when compared to the next most northerly record (the type specimen, at 20°S), there is some doubt about the identification.

SC/40/O 22 reported 10 sightings of 35 individuals in the area bounded by 30-40°S and 70–100°E from February to March, 1988. Joyce presented a summary of 407 sightings from IDCR cruises in 1978–1987. Goodall reported several new stranding records for South America.

5.4.2 Abundance

There is no population estimate. Joyce reported that it was the ziphiid most often sighted during the IDCR cruises. It was sighted about as often as Gray's beaked whale, *Mesoplodon grayi*, in the Indian Ocean north of 40°N (SC/40/O 22).

5.4.3 Migration

No information.

5.4.4 Life history

The maximum size reported in the literature for males is 694cm and for females 745cm. Goodall reported larger specimens of both sexes: a 714cm male with 50+ GLGs and a female of 750cm. She also reported an age of 37 GLGs for a 576cm female. A 780cm female contained a 185cm fetus (Baker, 1983). A 570cm female was lactating (Zemskii and Budylenko, 1970). A calf of 291cm had fetal folds (Ross, 1984).

Stomach contents of nine specimens included remains of squid of several families (Clarke, 1986) and krill (which may have been eaten by the squid).

5.4.5 Exploitation

Although there has been no fishery for the southern bottlenose whale, a few have been taken by pelagic whalers for research purposes (Tomilin and Latyshev, 1967; Zemskii and Budylenko, 1970).

5.4.6 Status

No information.

5.5 ? Hyperoodon sp.

Evidence has grown concerning the existence in the tropical Pacific of a beaked whale of unknown identity that is likely to prove to be a species of *Hyperoodon* (Leatherwood *et al.*, 1982). Two papers presented at this meeting dealt with this problem: SC/40/SM9 and SC/40/SM14. The consensus of the members of the sub-committee is that the whale is *H. planifrons* or may prove to be a new species. The records of *H. planifrons* from northwestern Australia (Flower, 1882) and from Brazil (Gianuca and Castello, 1976) make it plausible that the unidentified whale in the tropical Pacific could be of this species. However, considering that this is either a most remarkable range extension for a reputedly antitropical genus or even possibly an undescribed species of ziphiid of a different group, the sub-committee **recommended** that an attempt be made to collect two adult specimens (a male and a female) in the western Pacific. The possibility of collecting biopsy materials for molecular studies was also raised, but there would likely be difficulty in collecting a sufficient number of samples from both the Antarctic and the western Pacific to resolve the identity of these whales. If such studies suggested differences, specimens would still be needed for taxonomic analysis and type material.

5.5.1 Distribution

SC/40/SM9 reported eight sightings of a total of about 280 individuals on the equator at 166°W (central tropical Pacific) and in the western North Pacific in the area bounded by 130–142°E and 20–34°N. SC/40/SM14 reported 7 sightings in the area bounded by 80–170°W and 5°N – 15°S, with a concentration in the area 90–120°W and 5–15°N during 1965–88.

5.5.2 Abundance

SC/40/SM9 did not give numerical relative abundance of this species but implied that it was relatively rare. SC/40/SM14 reported that the species is rare, being involved in only 7 of 946 sightings of ziphiids.

5.5.3 - 5.5.6

There is nothing known concerning migrations, life history, exploitation or status.

5.6 Ziphius cavirostris

5.6.1 Distribution and stock identity

Cuvier's beaked whale is known from strandings along most coasts and many oceanic islands within all ocean basins (Heyning, in press). Strandings occur from tropical to sub-polar waters. Sightings data from the eastern tropical Pacific (SC/40/SM14) indicate that the species is found offshore to beyond the continental slope in this region.

Due to the wide geographical range and extreme sexual dimorphism in the skulls of *Z. cavirostris*, there are numerous synonyms in the literature (Hershkovitz, 1966; Heyning, in press). Although most of the variation observed in skulls is regarded as sexual dimorphism and/or individual variation, no comprehensive study has been done. Mitchell (1968) examined skeletal material from the northeast Pacific and believed that there are no separate stocks in that region.

5.6.2 Abundance

There are no abundance estimates for any region. Stranding data from the Northern Hemisphere indicate that strandings of *Z. cavirostris* are about as frequent as the strandings of all other ziphiid species combined (SC/40/SM21). Data from the eastern tropical Pacific (SC/40/SM14) suggest that sightings of *Z. cavirostris* are about as frequent as sightings of all species of *Mesoplodon* combined in that region. *Z. cavirostris* is the most frequently sighted medium-size cetacean within this region.

5.6.3 Migration

There is no information on migration for this species. Stranding and sighting data should be further analysed for seasonal trends in geographical distribution.

5.6.4 Life history

Life history data for this species are discussed in SC/40/SM22 and SM23. The maximum lengths recorded from precisely measured specimens are a 660cm female (Nicol, 1987) and a 693cm male. Contrary to prior published reports (Omura *et al.*, 1955), there seems to be no significant sexual dimorphism in adult size for this species (Heyning, in press).

Based on limited data, males seem to become sexually mature at about 11 GLGs in the dentine. The shortest sexually mature specimen was 526cm long and was also physically mature. The testes of sexually mature males are about 20cm in length and weigh from 150 to 372g each. The testis weights reported by Omura *et al.* (1955) seem an order of magnitude too large when compared to other data from *Z. cavirostris* and other ziphiid species of similar size. There is less reproductive information for females. The shortest sexually mature female was 512cm long. Males reach an age of up to 47 GLGs, but females attain an age of only 28 GLGs. The difference is not due to readability of layers. This vast difference in age between males and females cannot be easily explained, but the phenomenon also occurs in *Hyperoodon ampullatus* (Benjaminsen and Christensen, 1979) and in *Berardius bairdii* (SC/40/SM7). Additional specimens of *Ziphius* need to be aged to determine if the great difference in ages of males and females is general.

In the eastern tropical Pacific, pods range in size from one to seven individuals, with most sightings of four or fewer individuals; there are two records of mass strandings for this species (Heyning, in press).

5.6.5 Exploitation

The Japanese formerly took *Z. cavirostris* in small-type whaling (Omura *et al.*, 1955; Nishiwaki and Oguro, 1972). This take has largely ceased, but Kasuya reported that an occasional animal may be taken. A few *Z. cavirostris* were taken in the former small cetacean fishery off the Lesser Antilles island of St Vincent (Caldwell *et al.*, 1971). There is no systematic direct take of *Z. cavirostris* at this time. Animals may be taken incidentally in offshore fisheries, but there are no data for this.

5.6.6 Status

No information.

5.7 Mesoplodon spp.

It was suggested that species within this group be discussed in a comparative manner because there are few data on any one species and because such factors as taxonomy and pigmentation (SC/40/SM6) are more usefully covered in an overall review. Review of most of the current knowledge regarding biology can be found in Mead (1984) and Ross (1984). The species *M. pacificus* is herein retained in the genus *Mesoplodon*, not separated into the monotypic genus *Indopacetus* Moore, 1968. It is felt that until the entire genus is reviewed, no single species should be removed.

5.7.1 Distribution and stock identity

The distributions of various species of *Mesoplodon* are summarised for the Northern Hemisphere in SC/40/SM21 and for the Southern Hemisphere in SC/40/SM23. Identification of *Mesoplodon* to species at sea is difficult and seldom made, especially in the Northern Hemisphere, because the pigmentation patterns are less distinctive than for many Southern Hemisphere species. Therefore, the known distributions of the species are based almost exclusively on stranding records.

M. bidens – Sowerby's beaked whale is endemic to the North Atlantic, with the majority of strandings occurring around the British Isles. A few records are available from the northwestern Atlantic that might be records of strays, and one record from the Gulf of Mexico clearly is of a stray individual.

M. bowdoini – Andrew's beaked whale is known from about twenty specimens from the Southern Hemisphere, primarily from strandings in Australia and New Zealand. The species may be conspecific with *M. carlhubbsi*, which would give the species an antitropical distribution.

M. carlhubbsi – If Hubbs' beaked whale is distinct from *M. bowdoini*, then it is endemic to the North Pacific, with the majority of strandings occurring from British Columbia to southern California.

M. densirostris – Blainville's beaked whale seems to be distributed in tropical and warm temperate waters of all oceans. Strandings are most frequently recorded along the east coast of the United States, but stranding collection effort is also high in this region. *M. densirostris* is occasionally sighted in the eastern tropical Pacific (SC/40/SM14).

M. europaeus – Although the type specimen of Gervais' beaked whale was recorded from the English Channel, the overwhelming number of strandings are from the southeastern United States and the Caribbean region. There are records of three specimens from the Ascension Islands in the South Atlantic.

M. ginkgodens – This relatively rare species of *Mesoplodon* is known from nine strandings in the North Pacific in warm temperate and tropical waters and one stranding in the South Pacific in the Chatham Islands. Three specimens of the ginkgo-tooth beaked whale were also taken in Chinese waters (Nishiwaki *et al.*, 1972).

M. grayi – Gray's beaked whale has a circumpolar Southern Hemisphere distribution that ranges from 30° to at least 53°S. Approximately half of the recorded strandings were along the coast of New Zealand. There is one record of a *M. grayi* stranded on the coast of the Netherlands.

M. hectori – Most of the strandings of Hector's beaked whale have occurred in cold-water regions of the Southern Hemisphere (Mead and Baker, 1987), but four strandings occurred along southern California beaches in the late 1970s (Mead, 1981) and may represent a small stray group. Some additional information on recent strandings, including a mass stranding of four animals, was presented (SC/40/SM18).

M. layardii – The strap-toothed whale has a distribution in cooler waters of the Southern Hemisphere that resembles the distribution of *M. grayi*. It is the most commonly stranded species of *Mesoplodon* in the Southern Hemisphere and second only to *M. bidens* worldwide. In Tierra del Fuego, strandings of *M. layardii* consist primarily of adults, whereas strandings of *M. grayi* include young animals (SC/40/SM19).

M. mirus – True's beaked whale was previously believed to be endemic to the North Atlantic, but is now known from several strandings in the Southern Hemisphere. In the western North Atlantic, this species ranges from the Bahamas to Nova Scotia. In the northeast Atlantic most strandings occur along the British Isles and in the Bay of Biscay. Southern Hemisphere strandings include specimens from South Africa, Australia and New Zealand. Slight cranial and pigmentation differences between the North Atlantic and Southern Hemisphere specimens have been documented and discussed by Ross (1984). These differences suggest that the two groups are distinct breeding populations.

M. pacificus – Longman's beaked whale is known from two skulls, one from Australia and one from Somalia. Based on this, an Indopacific distribution is suggested.

M. stejnegeri – Stejneger's beaked whale is endemic to the North Pacific and is recorded from the Sea of Japan and along the Aleutian Islands to the coast of North America from Alaska south to southern California. The majority of strandings occur in the northern part of the range where it is not sympatric with *M. carlhubbsi*.

The unidentified species of *Mesoplodon* that has been sighted in the eastern tropical Pacific (Pitman *et al.*, 1987; SC/40/SM13 and 14) was discussed in detail. It was suggested that the basic colour pattern is similar to that of *M. layardii* (SC/40/SM21). Photographs of the unidentified species were compared with those of known *M. layardii* specimens from the Southern Hemisphere. It was concluded that although the basic pattern was similar, the differences are too great to consider the unidentified species to be *M. layardii*. The colour pattern of the unidentified species is not identical to that of any known species of ziphiid for which the colour pattern is known (the external appearance of *M. pacificus* is unknown).

5.7.2 Abundance

There are no data on absolute abundance for any species of *Mesoplodon*. The little relative abundance data available have been discussed in the above distribution section.

5.7.3 Migration

There is little or no good information to support or refute any migration pattern for any species of *Mesoplodon*.

5.7.4 Life history

There is very little life history information for any species of *Mesoplodon*. Most of the current information was summarised by Mead (1984) for all species and by Ross (1984) for those occurring in South African waters. The most information for any one species is for *M. carlhubbsi* (Mead *et al.*, 1982). Unless otherwise stated, all information in this section is from these papers.

M. bidens – Adult males may attain a length up to 550cm and females 505cm. The length at birth is about 240cm.

M. bowdoini – The largest specimens were a 457cm female and a 467cm adult male (SC/40/SM23).

M. carlhubbsi – The largest specimens of both sexes were 532cm in length. Calves are about 250cm long at birth, and the calving season is early summer (Mead *et al.*, 1982; Heyning, unpublished data). The mean testis weight of a 496cm sexually mature male was 250g.

M. densirostris – The maximum lengths recorded are for a 473cm male and a 471cm female. Calves are probably less than 240cm long at birth. The oldest physically immature male had 7 GLGs. The youngest physically mature female had 10 or 11 GLGs.

M. europaeus – The largest male was 520cm long and the largest female 456cm. Calves are about 210cm long at birth. The known maximum age for this species is 27 GLGs (Perrin and Myrick, 1980).

M. gingkodens – The maximum length reported for a female is 490cm and for a male 477cm. The maximum testis weight for a mature male was 140g (Nishiwaki *et al.*, 1972).

M. grayi – The largest female recorded was 533cm long and the largest male 564cm long. The shortest calf was 237cm long (Goodall and Baker, pers. comm.).

M. hectori – The largest male was 430cm long and the largest female 443cm. The shortest calf measured 210cm. The weight of a testis from a mature male was 116g. Two physically mature specimens (a male and a female) had nine GLGs in their teeth.

M. layardii – This is the largest known species of *Mesoplodon*. The males attain lengths up to 584cm and females 615cm. The shortest recorded calf was 250cm long (SC/40/SM20). McCann (1964) provided details on the reproductive tract of one female.

M. mirus – Females reach 510cm in length and males 533cm. Calves are about 233cm long at birth. The testis of a mature male weighed 170g. One South African female had 7 corpora in the right ovary and 6 in the left (Ross, 1984).

M. pacificus – This species is known from two skulls; thus there is no life history information available.

M. stejnegeri – The largest specimens of both sexes measured 525cm. The three known calves averaged about 245cm in length; they stranded at the southern edge of the range, two in California and one in Oregon (Heyning, unpublished data).

5.7.5 Exploitation

There are no known direct fisheries on any species of *Mesoplodon*. Rarely, some animals have been taken in small-type whaling (e.g. Nishiwaki and Oguro, 1972; Nishiwaki *et al.*, 1972). Some animals are incidentally taken in gillnet fisheries (Nishimura and Nishiwaki, 1964; Diamond *et al.*, 1987). The magnitude of this problem is unknown at this time.

5.7.6 Status

There are no data on the status of any species of *Mesoplodon*.

5.8 Tasmacetus shepherdi

5.8.1 Distribution and stock identity

Shepherd's beaked whale is found only in the Southern Hemisphere and seems to be associated with cooler waters from 33° to 50°S (SC/40/SM19 and 23). Best reported that there are now some specimens in South African museums.

5.8.2 Abundance

There is no information on abundance. However, because this species is only known from about twenty strandings and a few sightings (SC/40/SM23), it may be less abundant than some species of *Mesoplodon*.

5.8.3 Migration

There are no data on migration.

5.8.4 Life history

The largest female was 660cm long and the largest male 700cm (Mead, 1984). The female was sexually mature.

5.8.5 Exploitation

There are no records of direct or incidental takes.

5.8.6 Status

No information.

5.9 General recommendations

1. *Non-lethal research*. The sub-committee **recommended** that the new techniques for studying living cetaceans, such as individual indentification using natural marks, which have proven successful for larger whales, be encouraged for application to the beaked whales, particularly where there are reasonably consistent concentrations of a well-marked species for which concern exists about population size and stock identity (e.g. the northern bottlenose whale, *Hyperoodon ampullatus* in the North Atlantic). Whitehead reported that such studies of the species will begin soon in 'The Gully' off Nova Scotia.
2. *Effects of gillnets*. The sub-committee **recommended** that offshore gillnet fisheries should be monitored to determine the nature and extent of impact on beaked whales.
3. *Sampling catches*. The sub-committee **recommended** that, when possible, beaked whales taken in direct fisheries be examined thoroughly by biologists to collect data and samples that can be used to estimate life history parameters.
4. *Strandings*. Because information on life history is so sparse for most of the beaked whales, the sub-committee **recommended** that efforts be made to collect full suites of data and specimens for all stranded animals.

6. NEW INFORMATION ON OTHER STOCKS

6.1 Dolphins associated with tuna in the eastern tropical Pacific (ETP)

The Committee last year noted recent increases in levels of incidental mortality in the international tuna purse-seine fishery in the eastern Pacific and expressed concern over estimated substantial decline in stocks of three species that may have occurred in the period 1975 to the early 1980s (*Rep. int. Whal. Commn* 38: 51). The sub-committee recommended that detailed analyses of possible sources of bias in the abundance estimates based on data collected aboard commercial seiners be carried out and that indices of abundance based on US research-vessel surveys be reported to the Committee this year (*Rep. int. Whal. Commn* 38: 121). The sub-committee noted that documents submitted this year do address these questions and wishes to thank the members involved for this response. The sub-committee received the documents and discussed them briefly but did not conduct a substantive review of the issue. It **recommended** that such a review be carried out at a future meeting.

6.1.1 Estimates of mortality

SC/40/SM2 gave estimates of total incidental kill of dolphins for 1987. The total estimate based on kill-per-ton was 115,000. These levels are high, although they represent a 12–20% reduction over the previous year (*Rep. int. Whal. Commn* 38: 51). The number of sets on dolphins was 35% higher than in 1986, so that the kill-per-set declined. Reasons for this reduction are (1) there were lower average catches of tuna per dolphin set in 1987; (2) sets were slightly shorter on average; (3) the proportion of sets on common dolphins was smaller; (4) the percentage of night sets was down; (5) the proportion of sets with zero mortality was higher; (6) the average number of animals left in the net after backdown was smaller; and (7) the average group size encircled by the net was smaller.

It was noted that international participation in the observer programme operated by the IATTC has increased markedly. Observers were placed on board 45% of trips by fleets of all flags in 1987. The US policy was to attempt coverage of all US trips in 1987. The coverage of the US trips in the analysis was 86%; the final figure will be about 95%. The next highest was Mexico at 28%. During the first few months of 1988, observers were placed on 43% of both Mexican and US trips.

Hall suggested that mortality might be reduced substantially through better application of existing rescue gear and techniques. Further reduction of the kill would probably require development of new technology, and he expressed the hope that such research initiatives would be launched. The sub-committee **recommended** that such research be undertaken.

Concern was expressed about the comparability of mortality estimates over years. Estimates in recent years have been generated by three different methods, dictated by the data available. As coverage of the international fleet has improved, it has been possible to use more sophisticated methods. R. Holt reported plans to examine the different methods by subsampling the 1987 database, which covers almost all of the US trips.

It was also noted that kill estimates would be most useful for purposes of comparisons with estimates of abundance if they were calculated on a stock-by-stock basis. For example, the IATTC estimates for the offshore spotted dolphin are not stratified into estimates for the northern and southern stock units used in management and in estimation of abundance. The sub-committee **recommended** that the estimates be stratified by stock.

SC/40/SM1 tabulated the sex, length and reproductive condition of the dolphins examined by observers aboard the seiners. Only about one quarter of the observed kill was sampled. It was noted that several kills of over 50 animals occurred in single sets and that complete suites of life history from such large series would be extremely valuable in population analysis. The authors explained the logistical difficulties involved in dealing with such large samples. The sub-committee **recommended** that the level of biological sampling be increased, possibly by allocation of funds for returning the carcasses from large-kill sets to research facilities and for subsequent processing.

6.1.3 US sightings surveys

SC/40/SM12 presented relative abundance indices by stock based on a 1987 survey. R. Holt also provided a table of estimates from 1986.

The estimates were generated under a number of options. Some of these are expected to result in biased estimates of absolute abundance but may yield more reliable estimates of trends. Large differences were noted between estimates for the two years (e.g., under one set of assumptions, 1,257,300 offshore spotted dolphins in 1986 and 2,070,000 in 1987, a change much larger than could be accounted for by biological increase). R. Holt suggested possible explanations but considered them to be unsatisfactory. The group noted a reciprocal relationship between the estimates for spotted dolphins (given above) and those for common dolphins: 1.8 million in 1986 and 0.6 million in 1987. This may indicate that sampling offshore-spotted-dolphin habitat changed relative to the sampling of common-dolphin habitat in 1987. The tracklines were nearly the same in the two years, but the habitats may have shifted.

Pooled estimates, as defined in SC/40/SM12, appeared more stable than weighted estimates. The large differences noted may be a result of variances being underestimated, for example if dolphin schools occur in concentrations. It is possible that survey tracklines tend to hit or miss ridges of density, leading to correspondingly high or low estimates. It is also possible that many animals that are within the survey region in one season are outside in another, since in some years the tropical habitat is larger than in others due to temporary global climatic shifts.

If problems with the estimates are a result of forming of local concentrations of schools, greater sighting effort should solve the difficulty. For example, the southern region might be ignored, and more effort distributed over the northern region. However, the argument that animals may move between south and north seasonally would not then be adequately considered. Stratification by oceanographic features was discussed, but it was not considered feasible at present, especially on the micro-scale that may be required. Another possibility might be to have larger surveys in alternate years. A possible source of bias might be the use of better observers, on average, with more experience available in the second survey relative to the first. R. Holt noted that further investigative analysis would be carried out to assess the impact of factors such as this, sea state, etc. on the abundance estimates.

6.1.4 Indices of abundance from data collected on tuna seiners

SC/40/SM3 is a revision and update of Buckland and Anganuzzi (1988) which was reviewed last year. The study differs from the previous paper in that stratification procedures were introduced in the estimation of two additional parameters: average school size and f(0). In a manner similar to stratification of encounter rates (which was not changed from last year), school size estimates were computed for 1° squares and pooled into strata of similar magnitude. The overall estimates of average school size were made as weighted averages of the within-strata estimates.

The estimation of f(0) included consideration of three variables likely to have an effect on the detection function: fishing mode (dolphin or non-dolphin fishing); use of birds as cues; and use of helicopters to make initial sighting. These variables were combined by computing principal components from data pooled by 1° squares; component scores were assigned to each square. The stratification scheme was then applied to the component scores.

Two alternative area specifications were used: the areas defined in Buckland and Anganuzzi (1988) and somewhat smaller areas proposed by Au, Perryman and Perrin (1979 – also used in SC/40/SM12).

In general, the results are similar to those presented in Buckland and Anganuzzi (1988). Estimates for most stocks were slightly lower, with fewer significant trends indicated. The estimates were presented as provisional by the authors, pending computation of complete bootstrap standard errors and inclusion of additional data for 1987.

It was noted that inclusion of information regarding fishing mode, use of helicopters in searching and birds as sighting cues resulted in a marginal improvement in the reliability of the estimates and alleviated some of the concerns about bias expressed by the sub-committee last year.

There was discussion about relative differences and similarities between the results of this study and those of SC/40/SM12. It was noted that estimates for all stocks except northern offshore spotted dolphins were comparable, and in the tuna vessel estimates it is this stock for which the 1983 (El Niño) estimate is anomalously low. Estimates for eastern spinner dolphins, whose range is entirely contained within the survey areas in all analyses in all years, were least variable and showed no anomalous dip in 1983. There was consensus that environmental variation was the likely cause of the variation in estimates. Pitman noted that the 1983 El Niño resulted in the death of 15 million sea birds in the ETP and that birds of these species are frequently used as sighting cues. This could explain in part the lower sighting rate of 1983.

It was also suggested that redistribution of dolphins could be responsible for part of the inter-annual variation observed, both in the estimates in this study and the research vessel estimates reported in SC/40/SM12. Redistribution within the ETP was considered more likely than major shifts to areas outside of the known historical range.

6.1.5 Recommendation

The sub-committee was concerned that the mortality of dolphins of the three major species remains high when compared with the most recent estimates of absolute abundance (Holt and Powers, 1982) and **recommended** that every effort be made to bring it down and to assess its impacts on the stocks. An attempt should be made to produce updated estimates of absolute abundance.

6.1.6 UNEP/IATTC courses in Latin America

Hall reported that courses in marine mammal biology and assessment have been given in several countries in Latin America. The courses were directed at graduate students and others involved or likely to be involved in future in marine mammal research and management, including acting as scientific observers aboard commercial seiners in the tuna fishery. The IATTC organised the courses; funding was provided by UNEP. Several members of the sub-committee were involved as instructors or students; they stressed the high quality of the educational programme and its potential value to future conservation and management of dolphins and other marine mammals. The sub-committee endorses the effort and hopes that it will continue.

6.2 Other cetacean/fishery interactions

Da Silva reported that the Brazilian Foundation for the Conservation of Nature (FBCN) with funding from WWF-US carried out a survey of incidental catches in an artisanal gillnet fishery in Atafona in northern Rio de Janeiro State. The fishing grounds extend for some 80km along the coast in waters usually less than 16km from shore. The fleet comprises 91 boats crewed by 280 fishermen and fishes gillnets 4–13m deep × 110–2740m long with 14cm mesh. From June 1987 to April 1988, 55 dolphins of 5 species were caught: *Sotalia fluviatilis*, *Pontoporia blainvillei*, *Steno bredanensis*, *Delphinus delphis* and *Stenella* sp. The dolphins were used as bait in a longline fishery. The research was carried out by L. Lodi and L. Capistrano of FBCN.

6.3 Putative occurrence of Burmeister's porpoise in the Indian Ocean

A specimen of *Phocoena spinipinnis* reported from Heard Island in the subantarctic Indian Ocean is actually a specimen of the spectacled porpoise, *Australophocaena dioptrica* (SC/40/SM17); several members of the sub-committee have examined large series of both species, and the revised identification is certain. Thus *P. spinipinnis* remains a species endemic to coastal waters of southern South America (Brazil [SC/40/ProgRep Brazil], Argentina, Uruguay, Peru and Chile). The occurrence of *A. dioptrica* at Heard Island fits in well with its previously known broad distribution in sub-Antarctic and southern cold temperate waters.

6.4 Harbour porpoise

SC/40/SM5 reported the results of experimental line-transect surveys of harbour porpoises in an area of high density in the Bay of Fundy. Simultaneous surveys conducted by teams of observers on top of the pilot house and in the crow's nest yielded different results. Some possible causes are the greater area searched from the crow's nest, avoidance of the vessel by the porpoises, better sightability of porpoises viewed from the higher elevation, and differential distribution of sighting effort relative to the vessel's course. Hohn noted that harbour porpoises in the eastern North Pacific did not avoid survey vessels except at very close range. Suggestions from the group for improving survey methods included larger observer teams and assigned sighting sectors. The point was made that the situation in the Bay of Fundy offers a good opportunity for experimental development of line-transect methodology because of the very high density of harbour porpoises, which allows fitting of a density function to the data from a relatively short survey or survey leg. The sub-committee **recommended** that the possibilities for such work be considered by those involved in development and design of the IDCR minke whale surveys.

Bjørge reported that a programme of research on the harbour porpoise has been initiated in Norway this year. The three-year research programme is in cooperation with scientists from Sweden (SC/40/ProgRep Sweden), Denmark and the Federal Republic of Germany (SC/40/ProgRep FRG). The primary objectives of the Norwegian programme are to study reproduction and feeding habits. Stock identity will also be investigated. Samples will be collected from incidental gillnet kills and from strandings. A similar programme is under way in the Netherlands (SC/40/ProgRep Netherlands). Sightings of harbour porpoises in the North Atlantic were reported in SC/40/O 9 and 10, SC/40/O 29 and SC/40/ProgRep Netherlands. A pilot survey of harbour porpoises was conducted along the English North Sea coast in 1988 (SC/40/ProgRep UK).

6.5 White whales and narwhals

SC/40/SM10 dealt primarily with line-transect theory. While the group believes that the paper does not contain information on line-transect methodology that is not available elsewhere, they believe that the data on duration of dive in the white whale contained in the paper are new and valuable.

SC/40/SM4 discusses recent harvests of white whales in Alaska and contains data and assessments that the Committee has repeatedly recommended be provided (e.g. *Rep. int. Whal. Commn* 32: 59, 31: 67). The sub-committee concurred with the recommendation of the authors' that the estimates of abundance and harvests be refined and further work carried out on stock identity; the estimated removals of up to 6.7% are large enough to cause concern about their sustainability.

Sightings of white whales in the North Atlantic were reported in SC/40/O 9.

6.6 Pilot whales

SC/40/O 42 reported on the satellite tracking of a pilot whale re-introduced into the wild. The whale was located 479 times over a period of 95 days during which it travelled over 7,500km; time and depth data were collected for over 192,000 dives. The very large quantity of data collected provide an opportunity for modelling experimental design for tracking other small cetaceans and the large whales.

Sightings of pilot whales in the North Atlantic were reported in SC/40/O 9, 10, 11, 15, 29 and 39 and in SC/40/ProgRep Denmark.

6.7 Other species

New information was also received on a mass stranding of melon-headed whales, *Peponocephala electra*, in Brazil (SC/40/SM11); on sightings of North Atlantic killer whales (SC/40/O 9, 10, 15, 29, 30), whitebeaked dolphins (SC/40/O 9, 10), white-sided dolphins (SC/40/O 10, 29), common dolphins (SC/40/O 15, 29, 39), bottlenose dolphins (SC/40/O 15, 29, 39), Risso's dolphins and false killer whales (SC/40/O 39), and *Stenella spp*. (SC/40/O 15, 29, 39); on eastern North Pacific killer whales (SC/40/O 31); on sightings of Dall's porpoise (SC/40/O 37; on molecular genetics of several small cetaceans (SC/40/O 40); on the possible causes of mass strandings (SC/40/O 13); on sightings, strandings and exploitation of several small cetaceans in South America (SC/40/ProgReps Argentina and Brazil). Much additional information on sightings and strandings of small cetaceans and on national research programmes was included in the various national progress reports (see Item 4). A great increase (two-or threefold) in the incidence of strandings, mostly of common dolphins, was reported for the French coast (SC/40/ProgRep France). The causes of this are unknown. An unexplained mass mortality of over 700 bottlenose dolphins occurred along the US east coast (SC/40/ProgRep US); the cause is under study.

7. OTHER BUSINESS

7.1 Takes of small cetaceans in 1987

Takes are summarised in Appendix 3.

7.2 UNEP meeting on small cetaceans

A small working group was set up to consider the UNEP meeting. The sub-committee received the group's report (Appendix 2) and **recommended** that the IWC cooperate in organising and conducting the meeting.

7.3 Nomenclature

The sub-committee notes the general acceptance in the taxonomic community of the change from *Globicephala melaena* to *Globicephala melas* (*Rep. int. Whal. Commn* 39: 117) and the placement of *Phocoena dioptrica* in a new genus *Australophocaena* (*Rep. int. Whal. Commn* 39: 122) and **recommended** that the Committee's 'List of Recognised Species and Common Names' be amended accordingly.

7.4 ICES

Bjørge reported that the ICES Marine Mammals Committee recently discussed the benefits of all member nations collecting and reporting data on strandings and incidental takes of small cetaceans.

7.5 Publication of documents

The following documents are recommended for possible publication in a special volume on beaked whales: SC/40/SM6, 7, 8, 9, 13 (possibly partially combined with 14 and/or 21), 14, 15, 16, 18 (in part), 19, 20, 21, 22 and 23. Other papers developed from working papers of the meeting will be included in the volume. Additional papers on life history, status and exploitation of the northern bottlenose whale will be solicited from I. Christensen, E.D. Mitchell and R. Reeves. A list of other papers recommended for publication in *Rep. int. Whal. Commn* 39 was submitted to the Editorial Board.

7.6 Priority topics for 1989 meeting

The sub-committee proposed to review the biology and status of phocoenid populations in 1989. The group will also note and discuss briefly new information on other exploited stocks and species.

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Appendix 1

AGENDA

1. Election of Chairman
2. Appointment of rapporteurs
3. Adoption of agenda
4. Review of available documents
5. Review of population biology and exploitation of beaked whales, Ziphiidae
    - 5.1 *Berardius bairdii* (sub-items repeated for each species below)
        - 5.1.1 Distribution and stock identity
        - 5.1.2 Abundance
        - 5.1.3 Migration
        - 5.1.4 Life history
        - 5.1.5 Exploitation
        - 5.1.6 Status
    - 5.2 *Berardius arnuxii*
    - 5.3 *Hyperoodon ampullatus*
    - 5.4 *Hyperoodon planifrons*
    - 5.5 *?Hyperoodon* sp.
    - 5.6 *Ziphius cavirostris*
    - 5.7 *Mesoplodon* spp.
    - 5.8 *Tasmacetus shepherdi*
6. New information on other stocks
7. Other business
    - 7.1 Takes of small cetaceans in 1971
    - 7.2 UNEP meeting on small cetaceans
    - 7.3 Nomenclature
    - 7.4 ICES
    - 7.5 Publication of documents
    - 7.6 Priority topics for 1989 meeting

Appendix 2

RECOMMENDATIONS ON ORGANISATIONAL ASPECTS OF UNEP'S PROPOSED MEETING ON THE STATUS AND PROBLEMS OF SMALL CETACEANS

A small group of participants in the small cetaceans sub-committee reviewed the proposal for this meeting (IWC/40/10 D) to determine the importance of its goals and the suitability of the proposed approach. It was agreed that the topics proposed to be addressed were both important and timely; the scope of the proposed topics was very broad, but that the breadth appeared to be important to meet the goal of providing a basis for developing an action plan that is global in scope.

There are several documents that address many aspects of the topics proposed for this meeting, but many are in need of updating. A useful approach for this meeting might be to have consultants prepare updated material for several of these existing documents, perhaps on a regional basis, in advance of the meeting. Such updates could be finalised during the meeting, especially with any additional information that participants might bring.

The identification of institutions that would be able to provide training opportunities for scientists from developing countries would be be met by identifying individuals in potential institutions early in preparation for the meeting, and inviting their participation. Participants from areas where problems have been identified, or where they are anticipated, should be identified so that the most current information is available, and so interest in these problems is developed.

Several of the fisheries where small cetaceans are taken incidentally may be subject to technological improvements to reduce kill levels. Other fisheries may require management. The meeting should attempt to identify technical and management approaches, and those problems that appear to require additional technical expertise.

The meeting should schedule sufficient time to determine priorities for actions on small cetacean problems on a global basis, and within the regional scopes used in reviewing the status of the populations.

The proposed meeting appears to be an important step towards improving our understanding of small cetacean problems, and toward developing approaches to their solution. The group noted that scientists involved in the IWC have considerable expertise in the topics proposed to be addressed, and in the problems involved in convening such a meeting, and recommends that the IWC cooperate in planning and conducting the meeting.

Based on this discussion, the group recommends the following agenda to be considered:

1. Review status of small cetacean populations globally
   — Develop regional status reports in advance
1.1 Evaluate effect of habitat degradation
— Review ICES IOC Unit organochlorides report and other reports
— Review information on other factors
— Add information from participants
1.2 Directed fisheries
— Review Reeves and Brownell report on harvested marine mammals not under international control
— Add information from participants
1.3 Incidental kill in fisheries
— Update Northridge FAO/UNEP report on fishery/marine mammal interactions
— Review results of proposed IWC gillnet workshop
— Add information from participants
2. Review technological and management needs
2.1 Review outlook for technological solutions
2.2 Review effectiveness of different management approaches
3. Develop global action plan to address identified problem
3.1 Identify priorities for regional problems
3.2 Identify priorities that relate to global problems
3.3 Identify approaches for training needed
— Institutions to provide training
— Methods to identify individuals who would benefit from training

Appendix 3

REPORTED CATCHES OF SMALL CETACEANS IN 1987

		Argentina[1]	Australia[2]	Canada[3]	Denmark[4]	France[5]	Iceland[6]	Japan[7]	Netherlands[8]	New Zealand[9]	Norway[10]	Sweden[11]	UK[12]	USA[13]	USSR[14]	Other	Total[15]
Baird's beaked whale, *Berardius bairdii*	D	–	–	–	–	–	–	40	–	–	–	–	–	–	–	–	40
Narwhal, *Monodon monoceros*	D	–	–	x	x	–	–	–	–	–	–	–	–	–	–	–	x
White whale, *Delphinapterus leucas*	D	–	–	–	x	–	–	–	–	–	–	–	–	–	34	–	34+x
False killer whale, *Pseudorca crassidens*	D	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	2
Killer whale, *Orcinus orca*	D	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	3
	L	1	–	–	–	–	4	–	–	–	–	–	–	–	–	–	5
Pygmy or dwarf sperm whale, *Kogia* spp.	I	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
Long-finned pilot whale, *Globicephalus melas*	D	–	–	–	1,422	–	–	–	–	–	–	–	–	–	–	–	1,422
	I	–	–	–	–	1	–	–	–	–	–	–	2	x	–	–	3+x
Short-finned pilot whale, *G. macrorhynchus*	D	–	–	–	–	–	–	386	–	–	–	–	–	–	–	–	386
	I	–	–	–	–	–	–	9+x	–	–	–	–	–	–	–	–	9+x
Dusky dolphin, *Lagenorhynchus obscurus*	D	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x[16,17]	x
	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x[16,17]	x
Pacific white-sided d. *L. obliquidens*	D	–	–	–	–	–	–	16	–	–	–	–	–	–	–	–	16
	I	–	–	–	–	–	–	189+x	–	–	–	–	–	5+x	–	–	194+x
Atlantic white-sided dolphin, *L. acutus*	D	–	–	–	76	–	–	–	–	–	–	–	–	–	–	–	76
White-beaked dolphin, *L. albirostris*	I	–	–	–	–	–	–	–	–	–	–	–	2+x	–	–	–	2+x
Peale's dolphin, *L. australis*	D	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x[16]	x
	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3+x[16]	3+x
Bottlenose dolphin, *Tursiops truncatus*	D	–	–	–	1	–	–	1,812	–	–	–	–	–	–	–	–	1,813
	I	–	3	–	–	–	–	4+x	–	–	–	–	–	38–52+x	–	–	44–59+x
	L	–	–	–	–	–	–	–	–	–	–	–	–	24	–	–	24
Spotted dolphin, *Stenella attenuata*	I	–	–	–	–	–	–	–	–	–	–	–	–	5,031–8,598+x	–	57,544–63,510[18]	57,544–63,510
Spinner dolphin, *S. longirostris*	I	–	–	–	–	–	–	–	–	–	–	–	–	2,226–3,546+x	–	22,135–25,072[18]	22,135–25,072
Striped dolphin, *S. coeruleoalba*	D	–	–	–	–	3	–	2,173	–	–	–	–	–	–	–	–	2,176
	I	–	–	–	–	–	–	76+x	–	–	–	–	–	3–8+x	–	3,401–3,789[18]	3,477–3,865+x
	L	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1
Stenella spp.	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x[19]	x
Common dolphin, *Delphinus delphis*	D	–	1	–	–	2	–	6	–	–	–	–	–	–	–	–	9
	I	–	–	–	–	1+x	–	34+x	–	1+x	–	–	–	246–1,525+x	–	19,324–22,463+x[18,19]	19,360–22,499+x
Northern right whale d. *Lissodelphis borealis*	I	–	–	–	–	–	–	261+x	–	–	–	–	–	–	–	–	261+x
Hector's dolphin, *Cephalorhynchus hectori*	I	–	–	–	–	–	–	–	–	8+x	–	–	–	–	–	–	8+x
Commerson's dolphin, *C. commersonii*	I	20+x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20+x
Black dolphin, *C. eutropia*	D	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x[16]	x
	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x[16]	x
Risso's dolphin, *Grampus griseus*	D	–	–	–	–	1	–	3	–	–	–	–	–	–	–	–	4
Franciscana, *Pontoporia blainvillei*	I	x	–	–	–	–	–	–	–	–	–	–	–	–	–	x[19]	x
Tucuxi, *Sotalia fluviatilis*	I	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x[19]	x
Rough-toothed dolphin, *Steno bredanensis*	D	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
	I	–	–	–	–	–	–	–	–	–	–	–	–	8–24+x	–	x[19]	8–24+x
Harbour porpoise, *Phocoena phocoena*	D	–	–	–	1	–	–	8	–	–	–	–	–	–	–	–	9
	I	–	–	–	x	–	–	21	7+x	–	3	17–140	85+x	200–300	–	13+x[20]	346–569+x
Burmeister's porpoise, *P. spinipinnis*	D	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x[16]	x
	I	3+x	–	–	–	–	–	–	–	–	–	–	–	–	–	x[16]	3+x
Spectacled porpoise, *Australophocoena dioptrica*	I	3+x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3+x
Dall's porpoise, *Phocoenoides dalli*	D	–	–	–	–	–	–	13,406	–	–	–	–	–	–	–	–	13,406
	I	–	–	–	–	–	–	816+x	–	–	–	–	–	–	–	–	816+x
Unidentified species	D	–	–	–	–	–	–	667	–	–	–	–	–		–	–	667
	I	x	15+x	–	–	–	–	294+x	–	–	–	–	2+x	319–392+x	–	x[19]	630–730+x
Sub-total	D	x	1	x	1,500+x	6	–	18,523	–	–	–	–	–	–	34	x[19]	20,064+x
	I	26+x	18+x	–	x	2+x	–	1,705+x	7+x	9+x	3	17–140	91+x	8,076–14,450+x	–	102,417–114,847	104,297–116,850+x
	L	1	–	–	–	1	4	–	–	–	–	–	–	24	–	–	30
Total		27+x	19+x	x	1,500+x	9+x	4	20,228+x	7+x	9+x	3	17–140	91+x	8,100–14,474+x	34	102,417–114,847	124,391–136,944+x

Notes to the Table

* Official statistics have been taken to be those provided in National Progress Reports or official catch records submitted to the Secretariat. Values given in scientific papers to the Committee are provided for information only and their sources indicated; these are given under the heading 'Other'. Catches have been presented by nation, rather than ocean area, except in the case of the data submitted by the IATTC for the eastern Tropical Pacific. In this case, the submitted estimated catches are not broken down by country but a summed total incidental catch for the following countries is given: Costa Rica, Ecuador, El Salvador, Mexico, Panama, Spain, USA, Vanuatu and Venezuela.

Key: D = direct take; I = incidental capture; L = live capture; x = catches known to occur but no current information available on levels.

Footnotes: (1) SC/40/ProgRep Argentina. (2) SC/40/ProgRep Australia. (3) SC/40/O 31. (4) SC/40/ProgRep Denmark, SC/40/O 31 and SC/40/BIWS. (5) SC/39/ProgRep France, SC/40/ProgRep France and Collet (pers. comm.). (6) SC/40/ProgRep Iceland. (7) SC/40/ProgRep Japan and SC/40/BIWS. (8) SC/40/ProgRep Netherlands. (9) SC/40/ProgRep New Zealand. (10) SC/40/ProgRep Norway. (11) SC/40/ProgRep Sweden: 17 reported and estimation of 75 to 140 per year. (12) SC/40/ProgRep UK. (13) SC/40/ProgRep USA and SC/40/SM1. (14) SC/40/ProgRep USSR and SC/40/BIWS. (15) The totals do not take into account the USA catches in the ETP for *S. attenuata, S. longirostris, S. coeruleoalba and D. delphis*, as those are included in the estimates for the whole ETP. (16) Goodall (pers. comm.). (17) Progress Report to IUCN by Gaskin *et al.*, 1987. (18) SC/40/SM2. (19) Da Silva (pers. comm.). (20) Deimer (pers. comm.).

8955

GILLNET PROBLEMS ON THE RISE

Gillnets are very efficient in catching fish. Unfortunately, they also kill other marine animals efficiently and indiscriminately. Gillnet fisheries are proliferating and expanding around the world, and the incidental kills of cetaceans (and pinnipeds, birds, turtles, sharks and undersized or non-target fish) are growing rapidly and getting increasing attention in conservation circles and in the media. The damage done by the thousands of miles of pelagic driftnets now in use has received the most attention, but similar problems exist in hundreds of coastal fixed-net fisheries, many of them in the less-developed nations, where data collection, management and enforcement are often extremely difficult. The problems of assessment and regulation are exacerbated by the fact that the international aid agencies have pushed gillnets as cheap, efficient, and suitable for artesanal fisheries.

In the coming year, the CSG will give major attention to gillnet problems. This will include preparation and submission of proposals for funding of projects listed in the Action Plan that relate to gillnets (about half of the 44 projects in the Plan) and organization of an international conference on the technical aspects of the problem (described below). Following are brief summaries of some of the relevant issues and events.

Italian gillnetters kill whales and dolphins illegally

A drift gillnet fishery for swordfish in the waters surrounding the Italian Peninsula is estimated to kill thousands of dolphins and hundreds of whales annually. In a recent report to the Scientific Committee of the IWC, Giuseppe Notarbartolo di Sciara of the Center for Cetacean Studies (Centro Studi Cetacei) headquartered in Milan described the results of a limited unofficial survey of stranded carcasses and animals found dead or entangled at sea. In 1988, 92 whales and dolphins were found entangled or dead on the beach with clear signs of having been entangled. These included 9 sperm whales, one Cuvier's beaked whale, 10 pilot whales, five Risso's dolphins, 8 bottlenose dolphins, 39 striped dolphins and 20 unidentified cetaceans. The survey was limited to only a small part of the area of the fishery. In addition to the fact that there is no organized monitoring of the fishery, most incidental catches are believed to be actively concealed by the fishermen, because they are illegal and because of a wish to avoid adverse publicity. One method used is to sink the carcasses by tying them to large stones. The populations of cetaceans in Italian waters have not been assessed, but there is concern that the large and unregulated kills may be more than can be sustained without decline in abundance in the long term, especially considering the many other environmental abuses affecting the Mediterranean. Additional problems caused by the swordfish gillnetters include the hazards to navigation of unmarked nets, abuse of emergency radio frequencies, and possibly depletion of the swordfish resource itself. The following petition to several ministries of the Italian Government and to officials of the European Community has been circulated jointly by several organizations, including the Center for Cetacean Studies, the Tethys Institute, WWF-Italy, "Marevivo", the CETACEA Foundation and others:

"ENOUGH WITH THE KILLING OF CETACEANS CAUSED BY THE SWORDFISH FISHERY!

> CONSIDERED THAT
> – alone among all Mediterranean Countries, Italy has allowed the massive proliferation of pelagic driftnet fishing activities, mainly used to capture swordfish, with a fleet numbering more than 700 vessels and with a total net length exceeding 15,000 km, i.e. almost twice the entire length of the Italian coastline;
>
> – this fishing activity causes every year, in the waters surrounding the Italian Peninsula alone, the incidental death of thousands of dolphins and hundreds of larger cetaceans belonging to various species, including several sperm whales;
>
> – fishermen, to protect their nets and to elude the Italian law which protects all cetaceans, brutally mutilate the dolphins that are caught still alive, and sink the drowned specimens to conceal them;
>
> – this non-selective fishing method is rapidly depleting the Italian seas of numerous species, also rare, and of the swordfish itself, which is often captured below the size permitted by the law, thus attracting the hostility of all other categories of fishermen;
>
> – these huge obstructions, often insufficiently marked, constitute a

constant and serious danger for navigation, especially for pleasure boats, causing numerous foreign yachts to desert the Italian seas; - the constant abuse and congestion, by the swordfish fishermen, of the emergency radio frequency (channel 16 VHF - 156.800 kHz) is a further cause of discomfort and danger for navigation;

– if appropriate and timely action is not taken, it is most likely that the cetacean populations of the Italian seas, already depleted and threatened by numerous other factors, will be at risk of extinction by the year 2000;

PETITION
that fishing with pelagic driftnets be promptly outlawed in Italy, and that the resumption of alternative fishing methods, of proven selectivity, be encouraged.

San Remo, 9 August 1989"

Further information can be obtained from G. Notarbartolo di Sciara, Centro Studi Cetacei, Museo Civico di Storia Naturale, corso Venezia 55, 20121 Milano, Italy (FAX 06 392 2940 1987) or Pier Lorenzo Florio, Director TRAFFIC(Italy), via Salaria 290, 00199 Roma (FAX 06 868334).

New Zealand and Australia ban driftnetters

In response to greatly increasing activity in the southern hemisphere by driftnet fleets from Taiwan, Japan and South Korea, the governments of New Zealand and Australia have banned drift gillnetting within their 200-mile exclusive economic zones and are urging other nations in the South Pacific to do the same. The bans extend to the possession of large drift gillnets by any fishing craft, trans-shipment of drift-net catches and port access to drift gillnet vessels. In a press statement issued in May, Deputy Prime Minister Geoffrey Palmer and several other ministers characterized the use of drift gillnets as "abhorrent", saying that "their impact on fish resources is vandalistic and can destroy the viability of fisheries industries in the South Pacific". The ministers also expressed their alarm at the disastrous consequences the nets had on marine mammals. They stated in relation to the enforcement of a possible cooperative ban throughout the South Pacific,

"To add teeth to these efforts, we are prepared to provide aerial surveillance supported by a naval vessel to maintain a watch on the operations of drift gillnet vessels and to patrol the EEZs of countries taking similar measures as us that request our help."

Australia had previously (1986) prohibited use of long drift gillnets off its northern coast because of dolphin kills in a fishery formerly operated there, mainly by Taiwan. In July, Prime Minister R.J.L. Hawke announced an expansion of the ban in his Statement on the Environment,

"We will extend the net length restriction to cover the whole of the Australian Fishing Zone, continue to deny access by driftnet vessels to Australian ports, except in cases of emergency, and prevent transshipment of fish caught by driftnets in the Zone."

He said further,

"Driftnetting is a global problem and there is an urgent need for international action to put an end to this barbarous form of fishing. Accordingly, Australia will press for a global ban on driftnet fishing."

The two Australasian nations thus join Canada, the U.S., Peru, Vanuatu, Fiji and American Samoa in prohibiting the use of large-scale commercial driftnets in their waters. To quote the Earthtrust report "Stripmining the Seas, A Global Perspective on Driftnet Fisheries",

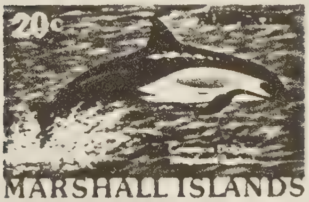
"Even Japan, which fields over half of the world's active driftnet vessels, has expelled these ships from its coastal waters, requiring by law in 1981 that squid driftnetters establish operations east of 170 degrees E longitude - more than 1000 miles from the Japanese mainland. This move was prompted when it became apparent that commercial squid driftnetters were not only threatening the livelihood of thousands of coastal fishermen, but promoting the collapse of Japan's offshore fisheries as well. This has not prevented the Japanese and others from seeking to establish driftnet fisheries in the coastal waters of other nations, or in international waters where the fleets freely operate without restriction."

The U.S. Government has recently taken a hard line with Japan, Taiwan and South Korea on the question of driftnetting on the high seas, in particular the North Pacific with its valuable and vulnerable salmon and albacore fisheries. Agreements for placement of observers aboard some vessels to collect data on catches of mammals, birds, turtles and undersized fish have been negotiated with all three nations. The agreements also call for the use of radio locator beacons to monitor the fleets, as well as containing provisions for gear restrictions, enforcement, bans on the catch of anadromous fish, etc. A bill introduced in the U.S. Congress in July 1989 (H.R. 2958) would require that the Secretary of State seek to secure an international agreement to ban the use of driftnets on the high seas.

Exploratory gillnetting kills whales and dolphins in Micronesia

The following is abstracted from the report of an observer on board the Japanese fishing boat *Monju Maru* during an exploratory drift-gillnetting trip in waters of the Federated States of Micronesia in February and March, this year.

The voyage was a joint venture between the Yap Marine Development Venture and the Monju Suisan Company Limited, authorized through a special arrangement between Japan and Yap State. The observer, Robert Goldblatt, was contracted by Yap's Marine Resource Management Division. The vessel was a 100-foot gillnet boat, carrying approximately 18 miles of nylon net separated into 9 nets approximately 2 miles long and 25 feet deep. The mesh size was 3 inches. The nets were set in the evening and pulled in the early morning, with total soaking time of 7-14 hours. The catch included skipjack tuna and other scombrid fishes (65% of the fish frozen and stored), billfish (42%), mahi mahi (24%), sharks (23%), manta rays, various small non-commercial fishes (16% of the total catch, all discarded), whales, dolphins, and turtles. Dolphins were caught in 19 of the total 24 sets made and whales in 3; the total catch was 97 dolphins (average 3 per set) and 11 whales (average about 1/2 whale per set). Ten turtles were caught, in 9 sets. The cetaceans were not identified to species. One whale was noted as weighing "several tons". The whales that could be handled by the winches were brought aboard and butchered, the meat being stored frozen for return to Japan. The dolphins were discarded. Dolphins still alive when the nets were pulled had their flukes cut off to facilitate removal from the mesh. Two leatherback turtles were released alive but injured; of the remaining 8 turtles (juvenile hawksbills and greens and one tentatively identified olive ridley), 4 were frozen (one alive), 2 were maintained alive on deck for later use, and 2 were discarded dead. Much of the fish catch was also discarded, because of undesirability, small size, damage by sharks, or decomposition due to prolonged time in the net.



The observer concluded in his report that the drift-gillnet method was wasteful and generally destructive of marine life and recommended strongly that no more permits be issued by the Federated States of Micronesia. Inquiries can be directed to Marine Resources Management Division, P.O. Box 251, Colonia, Yap 96943, Federated States of Micronesia.

The vaquita still needs help

The plight of the vaquita, the endemic porpoise restricted to the upper Gulf of California (*Phocoena sinus*) and arguably one of the least known and most endangered cetaceans, is receiving more attention in the Mexican press, but incidental kill in the gillnet fisheries in the Gulf is still not being monitored on a regular basis. A grant to the Mexican organization CEDO from the Center for Marine Conservation in 1988 allowed a pilot monitoring effort (Anon, 1989c). They interviewed a sample of the fishermen that operated 816 boats fishing in the same areas, at the same depths and during the same seasons that vaquitas are captured and found that 93% used the type of gillnet that entangles vaquitas. CEDO recommends the suspension of all gillnet fishing, especially the use of 5 and 6-inch mesh nets, in the northern Gulf of California.

Omar Vidal of the Guaymas Campus of the Instituto Tecnológico y de Estudios Superiores de Monterrey (ITESM) reports efforts to educate the public and government officials about the uncertain future of the species. A lengthy illustrated article by Vidal and other staff of the institute appeared recently in 10 newspapers scattered throughout Mexico. However, severe funding limitations prevent the research needed to adequately assess the size and impact of the gillnet kills and to determine what might be done to reduce them. Illegal gillnetting for the totoaba (a large sciaenid fish, itself endangered) and legal fisheries for sharks and other species continue at many localities around the upper Gulf and are largely unmonitored.

Greg Silber, a graduate student at the Institute of Marine Sciences of the University of California at Santa Cruz, writes in a letter to the Editor (October, 1988),

"I endorse the group's opinion that the biggest threat to the porpoise is that of totoaba gillnetters. In the coming months I will complete data analysis of four seasons of field work on the porpoise. My principal interest is the study of the relative abundance, ecology, and behavior of the porpoise (we have now accumulated 47 sightings of the vaquita), and not in interviewing fishermen or quantifying the fishing effort. Nonetheless, it is apparent that the vaquita population continues to receive considerable impact from this source. In the 1988 season alone we recovered three vaquita carcasses, two of which were gillnet victims, and the third may [also] have died as a result of entanglement. Opportunistic conversations indicate that fishermen are well aware of the vaquita and openly acknowledge that they entangle the porpoise in their nets.

"It is my hope that my work might shed new light on the ecology and distribution of the vaquita, such that future gillnet fishing might be restricted to locations where the vaquita is not present."

Silber's work has been supported by the Nature Conservancy's international program and the Center for Marine Conservation.

The population size is unknown but probably very small, possibly less than one hundred but also possibly a thousand or more (Barlow, 1986; Silber, 1987a and b, 1988a and b); the information required to make a reliable estimate does not exist. Survey conditions are very difficult in the turbid upper Gulf, and the porpoise's unobtrusive habits make finding and counting them even more difficult. The external appearance of the animal was not even well known until 1985 (Brownell et al., 1987). The CSG has given highest priority in its Action Plan to the need for monitoring the scattered gillnet fisheries in order to estimate incidental mortality. Following one year of fishery monitoring, a report would be submitted to the Mexican government, with recommendations for fishery management actions and an educational program to increase lay awareness of the uniqueness of this endemic Mexican species and the threat to its survival. The cost estimate for one year of monitoring, data collation, and preparation of the report is $20,000. Funds for this crucial work are currently not available in Mexico. Mexican cetologists stand ready to begin the monitoring as soon as international support can be found.

Further information can be obtained from CSG member Luis A. Fleischer (Centro de Investigaciones Pesqueras, Km1 Carretera a Pichilingue, La Paz, B.C.S., Mexico), Greg Silber (Institute of Marine Sciences, University of California, Santa Cruz, California 95064, U.S.A.) or Omar Vidal (Escuela de Ciencias Maritimas y Alimentarias, ITESM, Apartado Postal 484, Guaymas, Sonora, 85400 Mexico).

Gillnets may threaten harbor porpoise in Canada and U.S.

After an examination of the nature, magnitude and impact of incidental catches of harbor porpoises by groundfish gillnets in the southwestern Bay of Fundy in 1986, Andrew J. Read and CSG member David Gaskin (1988) at the University of Guelph concluded that, given the slow reproductive rate of the harbor porpoise, the incidental catch of around 100 per year in combination with other takes seriously threatens the population of the species in the region. Porpoises in the Bay of Fundy and Gulf of Maine apparently form a discrete population unit. Since 1973, two significant changes in length frequencies have occurred (an increase in length of calves and an absence of large porpoises in the 1986 sample). These changes may be attributable to the gillnet fishery, which has been operating for 10-15 years. Porpoises from the same population are also caught in other gillnet fisheries in the Gulf of Maine; data to support reliable estimation of the incidental kill there do not exist, but the kill may lie between about 300 and 800 (Polacheck, 1989). The University of Guelph studies suggest that this may be affecting the population of 5,000-18,000 adversely, but better population estimates are needed. Research to develop reliable census survey techniques is underway by the U.S. National Marine Fisheries Service (Polacheck, 1989). On the other side of the border, Canada's Fisheries and Oceans department seems little interested in addressing the problem of incidental porpoise kill.

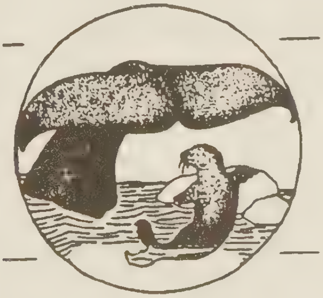
Comments by Tom Polacheck on the problem of conflict between porpoises and gillnet fisheries are trenchant and worth quoting *in extenso,*

"One avenue of porpoise protection is gear modification that might reduce or eliminate the incidental take, such as making the nets more 'visible' to the porpoise sonar system. Similar research in other fisheries with other small cetaceans has not been successful in the past [see article below], but one always remains hopeful."

"If it is true that harbor porpoises are attracted to the gillnets as a source of food, then eliminating or reducing the incidental kills would most likely require seasonally prohibiting gillnetting on many of the fishery's best grounds. Such an action could threaten the viability of the fishery.

"The problem of the incidental take of harbor porpoise exemplifies some of the problems that face both the marine scientist and society with regard to the interaction of marine mammals and commercial fisheries. Both are highly valued and represent issues of concern to various segments of society. The total number of animals killed may not appear large to some, and fishermen may find it hard to believe that their incidental takes are of any significance. However, the populations of small marine mammals tend to be highly vulnerable to low levels of exploitation (article, pp. 5-11). On the other hand, commercial fisheries represent peoples' livelihoods and way of life. Fisheries, particularly those operating at small scales, often cannot sustain large additional costs and remain competitive.

"As critical as the need for more information may be, resources for research are scarce and many important projects compete for limited funds. Population biology studies of marine mammals are expensive compared to those of land mammals, and the information required for assessment calls for long-term studies. Moreover, even the best possible assessments are likely to be imprecise, leaving large uncertainties. Yet, these difficulties should not be used as an excuse to do nothing. On conservation issues, ignorance has too often resulted in inaction. Competing concerns need to be balanced, and reasonable solutions found."



Modifying gillnets may not help

In a review recently submitted for publication in a technical journal, Steve Dawson of Canterbury University in New Zealand has concluded that net modifications tried to date have not been successful in reducing entanglement of cetaceans in gillnets and that reductions in mortality are best achieved through closure of specific areas to gillnetting. He discussed the methods and results of unsuccessful attempts to reduce entanglement through net modifications in the Japanese salmon gillnet fishery in the North Pacific (which takes mainly Dall's porpoise), in the now defunct Taiwanese shark fishery in waters of Northern Australia (which took tropical dolphins), and in South Africa, where gillnets used to protect bathing beaches kill bottlenose dolphins and other dolphins.

Most of the attempts to reduce entanglement through net modification have involved trying to make the net more "visible" acoustically to the animals, by the use of acoustic reflectors, such as air bubbles trapped in the net twine or attachment of air-filled tubing, and sound emitters. Dawson argues that since experimental work has shown that small cetaceans such as harbor porpoise can easily detect even unmodified nets, they become entangled not because their sonar system cannot detect the nets, but because they make mistakes that sometimes result in entanglement. He posits two kinds of possible mistakes: the animal may have an acoustic search image of what it expects to encounter and therefore not perceive non-target objects or pingers, or it may not be using its sonar and therefore be unaware of the net's presence. Dolphins and porpoises are certainly capable of learning to be on the lookout for warnings of the presence of nets, but the animals that blunder into nets of course usually do not survive to make use of their experience. In addition, there is the problem that the cetaceans may feed on the gillnet-caught fish or on the other scavengers feeding on them. In this case, a sound-emitter is efffective a "dinner bell" and may actually increase entanglements.

Dawson concludes that because "making nets more acoustically reflective and placing warning devices in them are unlikely to achieve better than marginal reductions in the entanglement rate of dolphins and porpoises",..."the management strategy most likely to achieve effective protection of cetacean populations from gillnet entanglement is the closure of specific areas to gillnetting.." He adds,

"Detailed data on the location of fishing effort, if available, can help identify which areas should be protected" ... "However, management decisions should not be based solely on such data."..."Management strategies must take into account that fishing is an extremely dynamic industry, and that the location and amount of fishing effort often change markedly between seasons. For this reason areas subject to low fishing effort may warrant inclusion into an area closure if they support significant marine mammal populations that would be at risk if gillnet fishing effort increased."

Steve Dawson's address is Department of Zoology, University of Canterbury, Christchurch 1, New Zealand.

International conference planned.

The long-awaited meeting on gillnets and cetaceans may finally materialize. The conference, to be titled Mortality of Cetaceans in Fishing Traps and Nets will be organized by the Scientific Committee of the IWC and is planned to take place in October, 1990 at the Southwest Fisheries Center in La Jolla, California. It will consist of a two-day symposium of invited and unsolicited technical papers and an invited workshop of 30 or so specialists. The main charges to the workshop will be:

(1) to identify and describe new and expanding net and trap fisheries which take cetaceans;

(2) to investigate how and why entanglement occurs;

(3) to the extent possible, estimate mortality and assess its impact on cetacean populations; and

(4) to consider possible ways of reducing levels of net-caused mortality of cetaceans.

The products of the workshop will include:

(1) a list and summary descriptions of gillnet and trap fisheries that take or potentially could take cetaceans, with lists of the species involved;

(2) a species-by-species summary, listing cetacean takes by population and fishery and assessing the impacts of the takes;

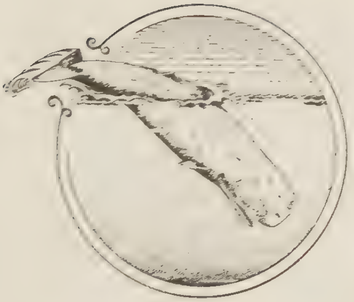
(3) an analysis of the causes of entanglement and assessment of technology and alternatives for reducing the incidental takes; and

(4) recommendations for (a) documentation of takes, (b) research to develop methods for reducing takes, and (c) management actions.

The estimated budget for the meeting is approximately $40,000. Most of this will be used to pay travel and perdiem costs for participants from the less developed nations and for a limited number of experts, such as a behavioral scientist, a sensory physiologist, and a gear expert. About half the needed funds have been pledged, by WWF-Sweden, the Government of New Zealand, the U.S. Marine Mammal Commission, the Southwest Fisheries Center of the U.S. National Marine Fisheries Service, and IUCN.

The IWC steering group for the meeting is presently trying to find the rest of the funds needed and preparing a draft list of invited participants. The IWC steering group includes Bill Perrin (U.S.), Bob Brownell (U.S.), Tom Arnbom (Sweden), John Harwood (U.K.), Linda Jones (U.S.) and Toshio Kasuya (Japan). The local organizing committee consists of Perrin, Brownell, Jones, Doug DeMaster and Jay Barlow.

It will be crucial to involve participants from the developing nations that are placing high priority on coastal and offshore fishery development. The amount of money that can be raised will determine how many of these people can be included. Anyone interested in helping support this important meeting should contact Bill Perrin as soon as possible (FAX 01 619 546 7003).



REPORT OF CSG CHAIRMAN TO MEETING OF IUCN SPECIES SURVIVAL COMMISSION
Rome, August 20-22, 1989

"This will be a short report. As some of you know, we issued an Action Plan last year, covering the 5-year period 1988-1992. The plan concentrates on the small cetaceans, because we believe that the greatest problems are there. Some of the small cetaceans are in imminent danger of extinction, in particular some of the river dolphins.

The plan list 44 specific projects and actions that the Group believes should go forward. Eleven are considered to be of the highest priority. Most of these (8) are concerned with river dolphins; the remaining three relate to the incidental kill of vaquitas in the Gulf of California, the illegal use of small cetaceans for crab bait in southern South America, and the need for a workshop on gillnets and cetaceans.

We cannot say that our progress in implementing the plan has been tremendous, but we can report some achievements for several of the recommended actions. I'll summarize these in the order in which the projects are listed in the plan.

> **Project 15.** We recommended that the status of the common dolphin in the western Mediterranean be assessed because of a possible great decline in the population there. This was to include research on the stock identity of dolphins in the western Mediterranean and the adjacent North Atlantic. Alex Aguilar of the University of Barcelona has received a grant from the National Science Foundation (NSF) U.S.-Spain Program to begin the work, using tagging and sighting surveys, and the first report will be due in October.
>
> **Project 35.** A high-priority project for the severely endangered baiji, or Chinese river dolphin, is to continue monitoring of the population. Prof. Zhou Kaiya of Nanjing Normal University has just informed me that he has received partial funding for this from WWF International.
>
> **Project 36.** Another of the high-priority items for the baiji is to determine individual movements and population structure. Bernd Wuersig of Texas A & M University has begun this work with funding from WWF, under a joint research agreement with the Academia Sinica and Nanjing Normal University. In addition, the International Whaling Commission (IWC) funded two Chinese students to attend the recent IWC-sponsored workshop on photo-identification methods for cetacean assessment, and they have returned to China and made a good start on cataloging the individual dolphins in the baiji population (about 300).
>
> **Project 39.** We are happy to report that good progress has been made toward saving Hector's dolphin, which is endemic to New Zealand. The New Zealand Government has established a sanctuary to protect the species from gillnetting and has started programs to monitor trends in abundance and to obtain better information on kill rates. This has been primarily due to the efforts of Steve Dawson and Elizabeth Slooten of Canterbury University in Christchurch, but international expressions of concern seem to have helped.
>
> **Project 40.** Very many of the problems that cetaceans face are caused by fisheries, and some of the worst problems are caused by gillnets. We recommended that an international workshop be convened to examine the problem of gillnets and cetaceans. We are very happy to announce that the meeting will take place in October, next year, in La Jolla, California. [See article above.]

The 44 projects listed in the action plan will cost about $1 million. So far, we've succeeded in raising only a small fraction of that. Ninety percent of the projects remain to be initiated. Many of these relate to situations where species or populations most definitely will disappear in this century unless there is intervention. The most severe crises are in the Indian Sub-continent and in China. The most recent news is that the susu has disappeared from the Karnaphuli River above the Kaptai Dam in Bangladesh, apparently because of poaching. This is a very large piece of habitat, now empty of dolphins. In another piece of grim news, it is estimated that construction of the proposed Three Gorges Dam on the Yangtze River will destroy dolphin habitat along 200 km of the river below the dam and reduce the carrying capacity of another 150 km of the river by 41-71%. And, of course, there is the recent information out of the meeting of the Scientific Committee of the IWC that the Antarctic population of the blue whale may be much smaller than had been previously estimated. [See article below]. The crisis for the cetaceans continues and grows. We need to move on these projects, and the Cetacean Specialist Group would very much welcome any assistance or advice on how to proceed." [Some advice was received; see article below on CSG's plans for stepped-up activities.]

RIVER DOLPHIN NEWS

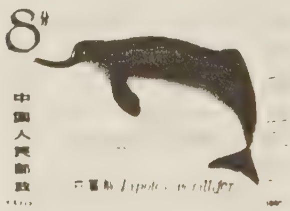
The CSG continues to place high priority on the severe problems faced by the river dolphins.

Susu studied in Indian reserve

In a paper submitted to TIGERPAPER, R. J. Rao, S. A. Hussain and R. K. Sharma reviewed research on the susu in the National Chambal Sanctuary, a crocodile sanctuary in Madhya Pradesh. A survey in the mid-1980s found 45 dolphins in a 305-km stretch of the Chambal River. Subsequent surveys by different teams recorded 43 dolphins in 265 km and, in 1988, 50 dolphins in 320 km. These numbers (all about 6 dolphins per km) are remarkably stable. The authors note that protection of crocodiles has also resulted in protection of dolphins. They recommend that enforcement of existing laws protecting dolphins and their habitat outside the reserve be improved. Further information is available from R. J. Rao, Deori Gharial Rearing Centre, National Chambal Sanctuary, P.O. Box 11, Morena, 476 001 M.P., India.

Baiji added to U.S. Endangered Species List

The U.S. Department of Interior's Fish and Wildlife Service has placed the severely depleted and baiji, *Lipotes vexillifer*, on the List of Endangered and Threatened Wildlife after a determination by the National Marine Fishery Service that the species is endangered. The action, effective June 29, 1989, gives the U.S. Government a mandate to assist China in planning for recovery of the species if that nation so requests. The other river dolphins *(Platanista gangetica, P. minor, Inia geoffrensis and Pontoporia blainvillei)* are under review for possible addition to the List.



Costs of the Three Gorges Dam outweigh benefits

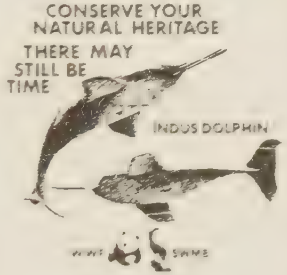
As noted above (Report of Chairman to meeting of SSC), construction of the proposed high dam at the Three Gorges on the Yangtze River (Chang Jiang) would destroy much of the habitat of the baiji. (See also last year's newsletter). A review in World Development by Philip M. Fearnside suggests that there would be other, perhaps unacceptable costs as well. The abstract of the paper follows: "China's plans for the Three Gorges Dam on the Yangzi River imply costs that go far beyond the dam's substantial monetary price. The consequences would be catastrophic should the dam fail as a result of warfare, earthquakes, or other causes. Resettlement of population displace by the reservoir, especially farmers, presents a formidable obstacle in the land around the reservoir site. Resettlement could affect minority groups if population is moved to border areas. The reservoir would sacrifice cultural landmarks. Erosion and reservoir siltation may impede navigation with a few years, and in the longer term will reduce storage volume. Impacts on natural habitats and human structures downstream of the dam include a variety of changes caused by greater streamflow at the low-water period and by reduced sediment load. The major justification for building the dam is flood control; alternatives include reforestation in the watershed, smaller dams on upper tributaries, and reversing the movement of population to dangerously exposed areas along the middle and lower Yangzi. Electricity could be produced more cheaply and quickly from smaller dams elsewhere. Energy conservation and population control are more cost effective ways of increasing per capita power supply. Installation of infrastructure

for construction at the damsite before impact assessment in complete raises doubts about the place of environmental evaluation in China's decision process." At last word in the press, the Three Gorges project was on hold, for unclear reasons but probably having to do with finances. The effects of the current purges on the young environmental movement in China are unknown.

Dam in Bangladesh causes local extinction of dolphins

The Ganges susu, *Platanista gangetica*, has disappeared from the portion of the Karnafuli River above the Kaptai Dam. A few dolphins remain in the estuarine region below the dam. The dam has created a permanent barrier across the river blocking the movements of the dolphins. The dolphins trapped above the dam were exposed to poaching, especially during the summer months, and have been exterminated. Fishermen in the region day that they have not seen dolphins above the dam for several years. Dolphins below the dam are also threatened, by heavy pollution, increased fishing activities and vessel traffic. Untreated domestic waste and discharges from metallurgical factories pollute the estuary. The maximum concentration of zinc found in the estuary is 0.5 mg/l. It has been observed that concentration as low as 0.3 ppm are lethal to snails and certain fishes. In a recent study of the hydrology of the estuary by Hossain and others, it was found that dissolved oxygen varied between 3.3 and 6.2 mg/l, whereas BOD ranged between 1.8 and 4.8 mg/l. All this indicates the degradation of the estuary that has occurred and the danger to wildlife there. The river dolphin workshop held in Wuhan, China in 1986 highlighted the dangers posed by construction of dams without giving adequate thought to impacts on dolphin populations and the riverine fauna in general. The results of the construction of the Kaptai Dam should be a warning to agencies planning construction of dams on other rivers inhabited by dolphins. The information cited here was obtained with the cooperation of residents of Chittagong and the banks of the Karnafuli.

—Submitted by CSG member R. S. Lal Mohan, B/18, Gandhinagar, Calicut, 673005, Kerala, India.



River dolphin volume published

The proceedings of the Workshop on Biology and Conservation of the Platanistoid Dolphins held at Wuhan, PRC in October, 1986 have been published in the Occasional Papers of the IUCN Species Survival Commission (No. 3, 173p). The volume contains the report of the workshop and 24 technical contributed papers on *Inia geoffrensis*, *Platanista gangetica*, *P. minor*, *Pontoporia blainvillei* and *Lipotes vexillifer*. Topics include population status, distribution, conservation, management, captive husbandry, acoustics, behavior, anatomy, ecology, and physiology. The book can be ordered from the IUCN Publications Services Unit, 219c Huntingdon Rd, Cambridge CB3 0DL, U.K. for U.S. $25.00 plus $4.38 for postage ($8.86 for airmail).

UPDATES

Peruvian dolphin fishery may be growing

In the past, the directed take in the Peruvian dolphin fishery has been mainly of dusky dolphins, *Lagenorhynchus obliquidens*, taken in drift gillnets, but other species are apparently becoming increasingly important. In addition, the total landings may be increasing. The catch in 1985 was approximately 10,000 dolphins and porpoises (Read et al., 1988). Detailed catch statistics by species are available for Pucusana, one of the important dolphin-fishing ports. In a paper in press and a recent draft report, Koen van Waerebeek and Julio Reyes list estimates of yearly landings there. (see table 1.)

The sharp increases in catches of dusky dolphins and Burmeister's porpoises are alarming. On one day alone, 106 dusky dolphins and 3 porpoises were landed. Government catch statistics for 1987 (reported by weight) do not indicate an increase in overall landings for Peru, but rather a 38% decrease. Either Pucusana is highly anomalous, or the official statistics are not accurate. It is not clear what, if anything, is being done officially to assess the impacts of the catches on the populations. A workshop scheduled for last November in Lima to bring together scientists and administrators interested in the fishery did not take place.

Table 1. L.o.= dusky dolphin; P.s.= Burmeister's porpoise (*Phocoena spinipinnis*), D.d.= common dolphin (*Delphinus delphis*), T.t.= bottlenose dolphin (*Tursiops truncatus*). * = included in Other.

Year	L.o.	P.s.	D.d.	T.t.	Other	Total
1985	95	47	*	*	14	175
1986	691	24	*	*	11	760
1987	711	83	264	30	12	1101
1988	1725	384	155	18	8	2290

Inquiries can be directed to Koen van Waerebeek, Laboratorium voor Morfologie en Systematiek der Dieren, Rijksuniversiteit Gent, Ledeganckstraat 35, 9000 Gent, Belgium, or Julio C. Reyes, Centro Peruano de Estudios Cetológicos (CEPEC), c/o Asociación de Ecología y Conservación (ECCO), Vanderghen 560, 2A, Lima-27, Peru.

Cetaceans receive increased protection in India

CSG member R. S. Lal Mohan reports that his efforts to obtain greater protection for dolphins and whales in Indian waters have succeeded. All species of cetaceans are now included in Schedule I of the Indian Wildlife Protection Act of 1972. They were formerly in Schedule II, Part 1. With the new status, sale of cetacean products is prohibited (under penalty of up to two years in prison and fine of up to Rs. 2000), and it has been possible to stop the sale of dolphin meat in the markets of Calicut.

Dolphin kills in the tuna fishery

Efforts to improve rescue performance by the international fleet of tuna seiners are paying off in lower kill rates, but increased fishing on dolphins in 1989 may result in higher kills for the year. Martin Hall of the Inter-American Tuna Commission provided information on technological extension work with the fleet.

1. A waterjet-propelled boat is being tested on some U.S. and non-U.S. boats to aid in herding dolphins to the backdown channel and in hand rescue; it can cross the corkline and is much better for these purposes than the inflated raft that has been used.

2. "Water hauls" to test the placement and alignment of small-mesh rescue panels in the net have been made for 30 boats so far this year. Some governments are requiring that prior to fishing under their flags, vessel captains attend a seminar on how to reduce dolphin mortality. These seminars are now frequently being attended by vessel navigators, deck bosses and fleet managers as well as captains. Nine seminars, in nearly all the countries involved in the fishery, have been held so far; 137 fleet personnel have attended, including 61 captains.

3. Many fishing companies are now routinely reviewing the dolphin-rescue performance of their captains after each trip. They are also collecting and collating performance data for release to interested parties.

4. The Mexican tuna industry has opened a tuna-dolphin office in San Diego, California. Carlos R. de Alba Pérez, formerly of the Universidad Autónoma de Baja California in La Paz, has been retained to head the office. Services to the Mexican fleet will include organizing training seminars, assisting boats in arranging net-alignment trials, maintaining monitoring inventories of dolphin-rescue equipment, and following captain performance in rescuing dolphins.

Based on preliminary and incomplete data for 1989, these and other efforts have resulted in drops in kill rates for the international fleet: a decline in kill per set of about 10% and in kill per ton of tuna of about 20%. These gains may not result in lower overall mortality, however, because fishing effort on dolphins is up steeply, about 38% in sets and 55% in tons. Unless the pattern of fishing changes drastically in the last two months of the year, the total kill in 1989 will be greater than in 1988. Questions can be directed to Martin Hall, IATTC, P.O. Box 271, La Jolla, California 92038, U.S.A.

CSG TAKES NEW STEPS TO IMPLEMENT ACTION PLAN

Two ideas emerged in recent consultations with IUCN Secretariat staff on how to speed up progress in implementing the action plan: to make each project the responsibility of an individual CSG member, and to set up an office for the CSG.

Assignment of projects to members--The member will be charged with the responsibility of preparing, or soliciting the preparation of, formal proposals to agreed potential donors. There will be agreed deadlines for preparation of the proposals. They will be subject to peer review by other, appropriate members of the CSG and will be forwarded by the Chairman to the potential donor, with a copy of the action plan and with a cover letter explaining that the proposal addresses a high priority for cetacean conservation as identified by IUCN. Not more than one proposal will be submitted the CSG to the same donor at the same time (unless more than one proposal has been specifically requested by the donor).

Office for the CSG--The expanded role proposed for the CSG will be much more active and involve a great deal of time and work. The time and resources that any one person can devote to the CSG are limited. The IUCN staff recommended strongly that core support be set up for the Group, most importantly to coordinate the preparation, review and submission of proposals, but also to carry out other functions, such as preparation and mailout of newsletters. They estimate that about $30,000 would be required annually for this; it would be mainly to hire some young cetologist with knowledge of the fund-raising world. The CMC is prepared to help with development of a proposal and with raising the funds for the core support.

New members of the CSG--Eight new members have been added to the Group during the year to augment expertise and relevant experience needed for preparation of proposals and for response to requests for advice by the IUCN Secretariat:

1. Fernando Rosas, Departamento de Biologia de Mamíferos Aquáticos, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil.

2. Ricardo Praderi, Sociedad Uruguaya Cetológica, Conchillas, Colonia, Uruguay.

3. George C. T. Chen, Graduate School of Fisheies, National Taiwan College of Marine Science and Technology, Keelung, Taiwan.

4. Jorge Oporto; Centro de Investigación y Manejo de Mamíferos Marinos (CIMMA), Universidad Austral de Chile, Valdivia.

5. Julio Reyes, Grupo Cetáceos, Asociación de Ecología y Conservación (ECCO), Lima, Peru.

6. John E. Heyning, Los Angeles County Museum of Natural History.

7. Idelisa Bonnelly de Calventi, Centro de Investigaciones de Biología Marina, Universidad Autónoma de Santo Domingo, Dominican Republic.

8. Aldemaro Romero, BIOMA (Fundación Venezolana para la Conservación de la Diversidad Biológica, Caracas.

New edition of the Action Plan--The Action Plan has been a best-seller; the printing of 1000 copies is nearly exhausted. An updated version will be published late this year or early next year. One project, a workshop to assess small cetaceans exploited by Japan, will be added; the appendices will be corrected and augmented; and a progress report will be included.

CMS TO FOCUS ON SMALL CETACEANS

The Convention on the Conservation of Migratory Species of Wild Animals (CMS), commonly called the Bonn Convention, aims to conserve migratory species by fully protecting endangered species and facilitating concerted action by Range States for migratory species which would benefit from international agreement. This necessarily involves more than one State, since a "migratory species", as defined in the Convention, is one "a significant proportion of whose members cyclically and predictably cross one or more national jurisdictional boundaries". The Convention came into force 1 November 1983 and currently has twenty-seven Parties: Benin, Cameroon, Chile, Denmark, Egypt, Finland, Federal Republic of Germany, Ghana, Hungary, India, Ireland, Israel, Italy, Luxembourg, Mali, Netherlands, Niger, Nigeria, Norway, Pakistan, Portugal, Senegal, Somalia, Spain, Sweden, Tunisia, United Kingdom, and the European Economic Community.

To encourage and oblige States to protect migratory species, the Convention takes two approaches, each reflected in a separate Appendix. (If the circumstances so warrant, a species may be listed in both Appendices). Appendix I lists species which are deemed "endangered", that is, which according to "reliable evidence, including the best scientific evidence available is in danger of extinction throughout all or a significant portion of its range" (in the context, equivalent to the IUCN category "endangered"). The Convention obliges Parties which are Range States of Appendix I species to prohibit their taking (hunting, capturing, etc) with few exceptions, to endeavor to conserve and restore their habitats, and to minimize activities and obstacles impeding migration and other factors endangering the species such as habitat loss and exotic species. Appendix I includes *Balaenoptera musculus, Megaptera novaeangliae, Balaena mysticetus*, and *Eubalaena glacialis*.

Appendix II lists species which would benefit from international co-operation, whether or not the species is endangered. Parties which are Range States of Appendix II species are required to endeavor to conclude AGREEMENTS, which must be open to accession by Range States which not Parties. Such AGREEMENTS can stipulate more precise and perhaps more onerous obligations than the global Convention, because they respond to a specific problem under definable circumstances. Appendix II at this point includes *Delphinapterus leucas* and North and Baltic Sea populations of *Delphinus delphis, Globicephala melas, Grampus griseus, Lagenorhynchus acutus, L. albirostris, Tursiops truncatus* and *Phocoena phocoena*.

The latter seven species were added to the Appendix at the October 1988 Conference of the Parties in Geneva, on the advice of the Scientific Council. The Conference also decided that the working group on small cetaceans established by the first Conference should be replaced by a working group of the Scientific Council. This working group is currently being established, and interested members of the Cetacean Specialist Group should contact the Convention Secretariat. CSG Chairman Bill Perrin was appointed to the Scientific Council by the Conference. The Scientific Council was directed to give priority over the next three years to a global review of the conservation status of small cetaceans, including freshwater species, to establish the case for Parties to prepare proposals for further additions of small cetacean species to Appendix II at the next Conference.

The Parties also stressed the need to complete work arising from their first Conference, including the development of the AGREEMENT for North and Baltic Sea populations of *Phocoena phocoena* and *Tursiops truncatus*. (It is possible that the AGREEMENT will be extended to include some other small-cetacean populations occurring in that area, following the amendment of Appendix II, as mentioned above).

Further information can be obtained from the Coordinator of the UNEP/CMS Secretariat (Judy Johnson), Postfach 201448, D-5300 Bonn, Federal Republic of Germany.

Submitted by UNEP/CMS Secretariat

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DAUPHIN DE COMMERSON
RF
TERRES AUSTRALES ET ANTARCTIQUES FRANCAISES

HOW MANY BLUE WHALES ARE LEFT IN THE ANTARCTIC?

There may not be as many blue whales remaining in the Antarctic as have been previously estimated. Certain other of the great whales may also be more depleted there than has been thought. The conclusions of a working paper submitted to the Scientific Committee of the International Whaling Commission in San Diego (Butterworth and Decker, 1989) this year have attracted a lot of attention and caused concern in the environmental community (e.g., see Anon, 1989a and b). However, the paper is preliminary; the authors emphasize that their conclusions are tentative and give several reasons why the estimates may be biased downward.

The estimates were developed from sightings data collected during IWC cruises to census minke whales in 1979-1986, using methodology similar to that used to generate estimates of minke whale abundance. A series of estimates were made for each species considered, using different data from different sighting modes and different combinations of survey years. The estimate of most concern is that of about 500 (with a coefficient of variation of 40%) for the blue whale. The estimates for other species (fin, sei, sperm, humpback, killer and pilot whales) are on the whole of less concern, either because they are not greatly lower than expected or because a significant portion of the range, or even most of the range in some cases, of the stock lies north of the area surveyed.

The Scientific Committee noted that the small number of sightings meant that the data could not be stratified nor estimates calculated by area, as has been done for minke whales, a factor affecting possibly both accuracy and precision. It was further noted that the estimates all require adjustment for the unsurveyed area (the surveys covered only 64% of the area south of latitude 60 degrees South and adjustment for whales missed on the trackline (a chronic problem with line-transect surveys). The Committee concluded that although the estimates suffered from these problems, they were very much lower than the total known catches from the stocks and concluded that at least the blue and fin whale stocks are at only a very small fraction of their unexploited size. Some members of the Committee expressed reservations about this statement for fin whales, because their range extends north of the survey area.

The most recent estimate of the number of blue whales in the Antarctic based on trends in catches was about 10,000 (including about 4,000 "exploitable" adult whales) in 1963 (Gulland, 1981). Earlier estimates were 930-2790 in 1961/62 (IWC, 1964) and 10,600 for Areas II-V for 1965/66 - 1970/71 (Chapman, 1974). The estimate of 4440 (south of 50 degrees S) in 1965/66-1976/77 by Masaki and Yamamura (1978) was based on sightings from Japanese whale-scouting vessels. An earlier estimate derived from the IDCR sightings data (for the first 6 years) was 1011 (with S.E. of 412) for 75% of the area south of 60 Degrees S (Butterworth and Dudley, 1984). Thus, while it is not clear with which prior estimate(s) the most recent estimate should be compared, the new estimate is lower than all previous estimates; there is no evidence that the blue whale has even begun to recover in the Antarctic, despite 20 years of complete protection.

As noted by NMFS Chief Scientist Michael Tillman in a letter to Ocean Science News, the IWC Scientific Committee had time at the meeting only to take a very cursory look at the estimates. Tillman concludes that "the utility of these estimates is in great doubt at this stage" and advises that judgment be held until the Scientific Committee has had time to examine the estimates and their derivation in detail. Caution would seem to be in order; in some quarters, more faith is being placed in the estimates than the authors themselves are willing to place in them. In any case, the estimates are not encouraging, and the topic most certainly will come up again at the IWC meetings in the Netherlands next year.

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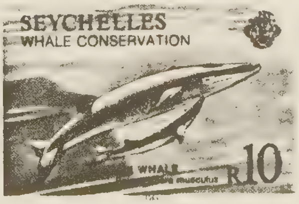

JAPAN PORPOISE CATCHES NOT SUSTAINABLE

Japanese catches of Dall's porpoise tripled from 1987 to 1988, possibly as a result of reduction in whale catches. The following is from the report of the IWC Scientific Committee for 1989:

"The Committee is extremely concerned about the great increase in take of Dall's porpoise in the Japanese hand-harpoon fishery, from about 13,000 in 1987 to about 39,000 in 1988 (SC/41/ProgRep Japan). There is evidence that the porpoise meat is being substituted in commerce for whale meat because of the decrease in access to large whales. The take is from two stocks in unknown proportion, estimated to contain about 105,000 porpoises in the aggregate..... There may be some over-reporting involved in the 1988 estimate, but other catches in an international gillnet fishery are not included. The Committee concludes that the present take is clearly unsustainable. Depending on the stock composition of the catch, the situation may be even worse for one of the stocks than immediately apparent.

"The Committee believes that it is urgent that the catch be reduced at least to the levels of previous years (which themselves may have been too high) and that assessments of status of the stocks be carried out, to determine safe levels of catch for the two stocks independently. It recommends that catch statistics be collected and reported on a stock-by-stock basis, and that the Republic of Korea be requested to report by-catches of Dall's porpoise (and other cetaceans) in its squid gillnet fishery to the IWC."

The IWC has chosen to demur on the question of management mandate for small cetaceans; currently it only allows its Scientific Committee (on a low-priority basis) to receive and review scientific information and make recommendations, which have no force and are not considered substantively in the Commission per se. Because of this international management vacuum and because of concern about rising Japanese catches of Dall's porpoise and other small cetaceans, the CSG is adding a project to its Action Plan:

"39. Convene workshop to assess small cetaceans exploited by Japan ($16,000)

Several small cetaceans may be seriously over-exploited in the western Pacific. In 1988 Japan took over 33,000 Dall's porpoise in harpoon fisheries. This is clearly unsustainable if the current estimates of the total population of the two or more stocks involved of about 110,000 is correct (IWC, 1989). Concern has also been expressed about increased takes of Baird's beaked whales and pilot whales. The small-cetacean meat is being substituted for large-whale meat in commerce as the Japanese access to the great whales declines. The small cetaceans are not managed by the IWC. Although national quotas have been set by Japan for beaked whales and pilot whales, these may be too high, and the Dall's porpoise take has been largely unregulated. A workshop meeting involving international small-cetaceans experts and experts in whale assessment and management is needed, to assemble and review the existing data, to identify and plan needed research to achieve adequate assessments, and to formulate recommendations for interim management."

RESIDENT BLUE WHALES OFF CENTRAL AMERICA?

Steve Reilly and Vicky Thayer of the Southwest Fisheries Center in La Jolla, California recently completed a study of blue whale sightings extracted from two decades of cetacean sightings by observers in the eastern Pacific and have concluded in a paper to be presented at the marine mammal conference in Monterey in December that a resident population of blue whales may inhabit waters off Central America. All 211 sightings of blue whales examined occurred in "relatively cool, productive upwelling-modified waters, along Baja California, the equator near the Galapagos Is., the coasts of Ecuador and northern Peru, and around the Costa Rica Dome (a large, stationary eddy centered near 9 degrees N, 89 degrees W). Occupation of the most productive parts of the ETP, all with relatively large standing stocks of euphausiids, indicates that blue whales may select low latitude habitats which also permit foraging. The waters off western Baja California were occupied seasonally, with a sightings peak coinciding with the spring peak in upwelling and biological production. The Costa Rica Dome area was occupied year round, suggesting either a resident population, or that both northern and southern hemisphere whales visit, with temporal overlap and potential for interbreeding." They propose that the identity of the whales in the Costa Rica Dome be determined by following the movements of individual whales, by photo-identification or satellite-based tracking. Further information can be had from the authors at P.O. Box 271, La Jolla, California 92038, U.S.A.

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A DWARF FORM OF THE SPINNER DOLPHIN (*STENELLA LONGIROSTRIS*) FROM THAILAND

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Abstract

A very small form of the spinner dolphin has been found to inhabit the Gulf of Thailand. Ten specimens taken incidentally in a local shrimp fishery differ from specimens of this species collected elsewhere in body size and shape, skull size and shape, number of teeth and numbers of thoracic and lumbar vertebrae. Four cranially adult males were 129–137 cm long, well below the ranges for the Indian Ocean, western Pacific, central Pacific, eastern Pacific and Atlantic. The skull is also very small. Tooth counts and vertebral counts average lower than in other series. The color pattern is not significantly different from that of spinner dolphins in the central and western Pacific, Atlantic and Indian Oceans but differs from that of the small eastern spinner of the eastern Pacific. The Gulf of Thailand specimens are morphologically separable from all other specimens, but it is to be expected that when larger samples are available there will be some overlap. The dwarf form may overlap in body and skull size with small spinner dolphins taken incidentally in a gillnet fishery for sharks off northern Australia. The geographic range of the dwarf spinner may be restricted. The size and status of the population and the impact of the shrimp fishery are unknown and should be investigated. The dwarf spinner may have an ecology different from that of other spinners, feeding mainly on reef-associated and benthic organisms rather than mesopelagic animals.

Key words: *Stenella longirostris*, dwarf spinner dolphin, Gulf of Thailand, morphometrics.

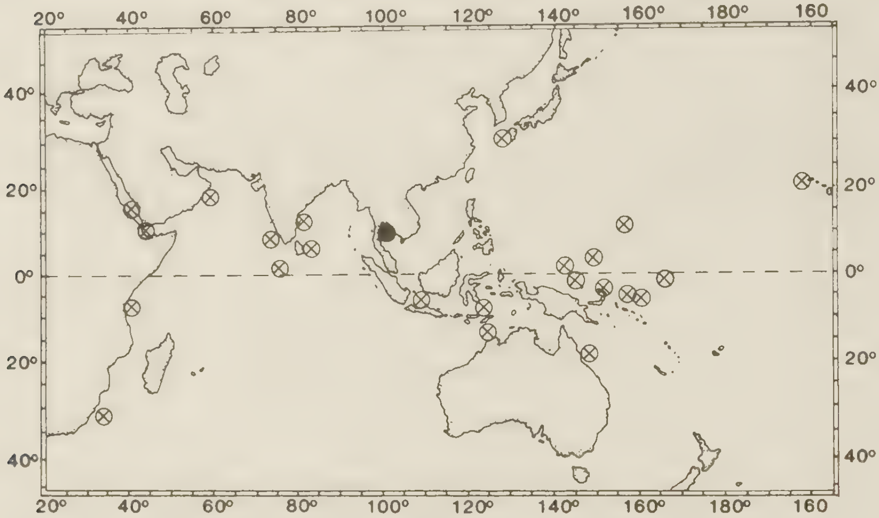


Figure 1. Approximate collection localities for *Stenella longirostris* in the Indopacific west of 160°W (Howell and Pearson 1977; Alling 1985; Miyazaki and Wada 1978; Masaki and Kato 1979; Mizue *et al.* 1964; Miyazaki 1986; Natarjan and Rajaguru 1983; Ogawa 1936; Mohan 1985; Robineau and Rose 1983; Hembree 1980, 1986; Gilpatrick *et al.* 1987). Solid symbol is in Bight of Bangkok. (See Gilpatrick *et al.* 1987 and Perrin and Gilpatrick, in press, for precise locations and other sighting localities).

Pronounced geographical variation in small odontocetes has been found to be the rule rather than the exception (Perrin 1984); this existence of numerous morphologically distinct populations has obvious and important implications for conservation and management of cetaceans (Perrin and Reilly 1984). The spinner dolphin occurs around the world in the tropics (Perrin and Gilpatrick, in press) and is involved in exploitation and conservation problems in several regions (Perrin 1988). The purpose of this paper is to report the discovery of a population of exploited spinner dolphins in the Gulf of Thailand that differ sharply in adult size and other features from spinner dolphins as previously described from other regions.

MATERIALS AND METHODS

The material examined consists of 10 specimens taken incidentally in shrimp trawls during night fishing in 1970–1971 in the Bight of Bangkok by small local trawlers (5–10 gross tons, 6–7 m) based at Sakhon in western Bangkok (Fig. 1). The dolphins were returned to port at the request of K. Morishima, who forwarded external photographs, external measurements (for 9 individuals), weights (for 7) and prepared skulls and postcranial skeletons to M. Nishiwaki at the Ocean Research Institute of the University of Tokyo. The material was later transferred to the National Science Museum, Tokyo (NSM, catalog numbers M24851, M24971–79). Skull and skeletal measurements and counts were taken as described in Perrin (1975). Specimens with all vertebral ephiphyses

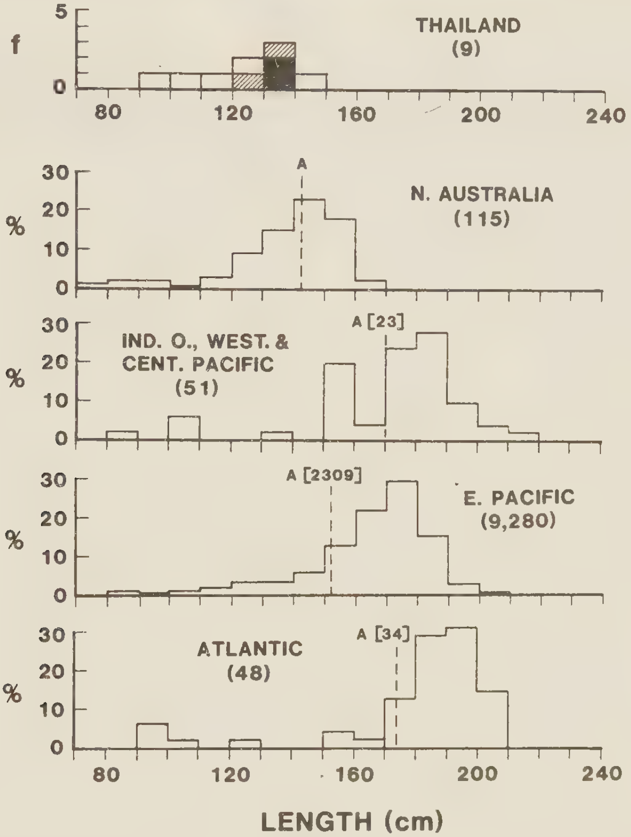


Figure 2. Comparison of distribution of body length and minimum adult length for males and females combined (A) in Gulf of Thailand specimens of *Stenella longirostris* with those for spinner dolphins from northern Australia (Hembree 1986), the Indian Ocean and western and central Pacific (see Fig. 1 for sources), eastern Pacific (unpublished data and Perrin *et al.* 1985), and Atlantic (sources listed in Perrin *et al.* 1981). Sample sizes in parentheses. Number of adults included in estimate of minimum adult size in square brackets. Solid rectangles represent physically mature specimens; hatched are sexually mature but not physically mature; open are immature or of unknown status.

fused to the centra (evidenced by absence of a visible seam at the surface) were judged physically mature. Distal fusion of maxilla and premaxilla was used as an approximate index of sexual and cranial maturity (Perrin 1975). Comparative data came from the literature and museum specimens. We also had access to three bodies of unpublished data. Length data and partial data on maturity and stomach contents for 115 spinner dolphins killed incidentally in a former Taiwanese gillnet fishery for sharks in the Timor and Arafura Seas off northern Australia are contained in a contract report to the Australian National Parks and Wildlife Service by the late Durant Hembree (1986). Length and maturity data for 9,280 spinner dolphins (of all stocks) killed incidentally in the tuna purse-seine fishery in the eastern tropical Pacific came from life-history data

Table 1. Ranges of selected external measurements (in cm) of adult spinner dolphins from Thailand, other regions in Indopacific, eastern Pacific and Atlantic, and maximum values for spinner dolphins from northern Australia. Data for other than Thailand specimens from Hembree (1986), Howell and Pearson (1977), Masaki and Kato (1979), Miyazaki (1986), Miyazaki and Wada (1978), Perrin (1975), Perrin *et al.* (1979, 1981, 1985) and unpublished data from K. S. Norris. Thailand specimens are males; sexes pooled for other areas. Sample sizes in parentheses.

	Thailand	Indopacific	E. Pacific	Atlantic	N. Australia
		(minimum and maximum)			(maximum)
Total length	129–137 (4)	172–209 (17)	152–235 (2,309)	173–208 (34)	158 (41)
Tip of upper jaw to:					
Apex of melon	14 (3)	15–19 (9)	11–17 (91)	13–20 (32)	—
Center of blowhole	22–27 (4)	32–38 (8)	25–36 (90)	30–39 (32)	—
Center of eye	25 (4)	29–35 (10)	26–35 (86)	30–36 (34)	31 (40)
End of gape	22–25 (4)	27–31 (9)	23–31 (92)	25–33 (35)	—
Anterior insertion of flipper	33–34 (4)	42–50 (8)	37–47 (92)	41–53 (35)	46 (40)
Umbilical scar	67 (4)	87–101 (9)	75–97 (92)	85–101 (23)	80 (39)
Anterior length of flipper	22–23 (4)	19–27 (10)	—	25–38 (34)	27 (40)
Posterior length of flipper	17–18 (4)	—	16–22 (83)	—	21 (40)
Width of flipper	8 (4)	9 (1)	—	8–11 (34)	11 (40)
Width of flukes	28–38 (4)	38–46 (9)	31–45 (84)	36–53 (33)	42 (39)
Height of dorsal fin	13–16 (4)	17 (1)	—	15–25 (34)	18 (41)

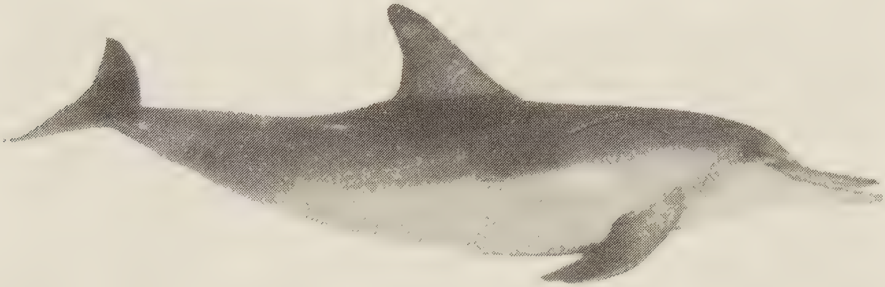


Figure 3. Dwarf spinner dolphin from the Gulf of Thailand (photograph not identified to specimen).

bases maintained in the Fishery/Marine Mammal Interactions Division at the Southwest Fisheries Center; length frequencies were computed using the program BMDP2R—Detailed Data Description of the BMDP series (Dixon *et al.* 1985). We also had access to data and specimens collected on the *Westward* cruise to the southeastern Central Pacific in 1970–1971, provided by K. S. Norris, University of California, Santa Cruz, CA 95064.

Comparative specimens examined—Eastern Pacific and Atlantic: listed in Perrin (1975) and Perrin *et al.* (1979, 1981) and SWFC 0025 (DAB 100) from 140°19′N, 93°10′W. Indian Ocean: Sri Lanka, 4 (BMNH 1891.10.13.2, 1948.4.20.1, 1949.10.27.1 and 2); Maldives, 5 (BMNH 1959.7.9.1, 3, 4, 5 and 6). Western Pacific: Japan, 1 (NSM M24800); between 5°N and 9°S and between 142° and 160°E, 5 (NSM M24930, M24931, M24933, M24934); Eniwetok, 1 (USNM 395404). Central Pacific: Hawaii, 28 (LACM 27093, 27095, 54049, 54050, 54056, 54057, 54060 and 72296; CAS 10529, 16455, 16456, 16457 and 16458; SWFC WFP 605, 606, 623, 669 and 671; MCZ 5170; USNM 339649 and 504140; MMBL 1194; NSM 24615 and 24815; BMNH 1965.8.25.1); Christmas Island, 2 (ANS 019194 and 019915); Washington Island, 1 (USNM 504251); Rangiroa (Tuamotu Islands), 1 (USNM 504252); Hiva Oa (Marquesa Islands), 1 (USNM 504253).

Museum acronyms—ANS, Academy of Natural Sciences, Philadelphia, Pennsylvania; BMNH, British Museum (Natural History), London; CAS, California Academy of Sciences, San Francisco; LACM, Los Angeles County Museum of Natural History, Los Angeles, California; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MMBL, U.S. Marine Mammal Laboratory, Seattle, Washington; NSM, National Science Museum, Tokyo; SWFC, Southwest Fisheries Center, La Jolla, California; UF, University of Florida, Gainesville; USNM, U.S. National Museum of Natural History, Smithsonian Institution, Washington, DC.

RESULTS

External size, shape and coloration—The adult Thailand specimens were on the average smaller than the specimens from northern Australia and below the

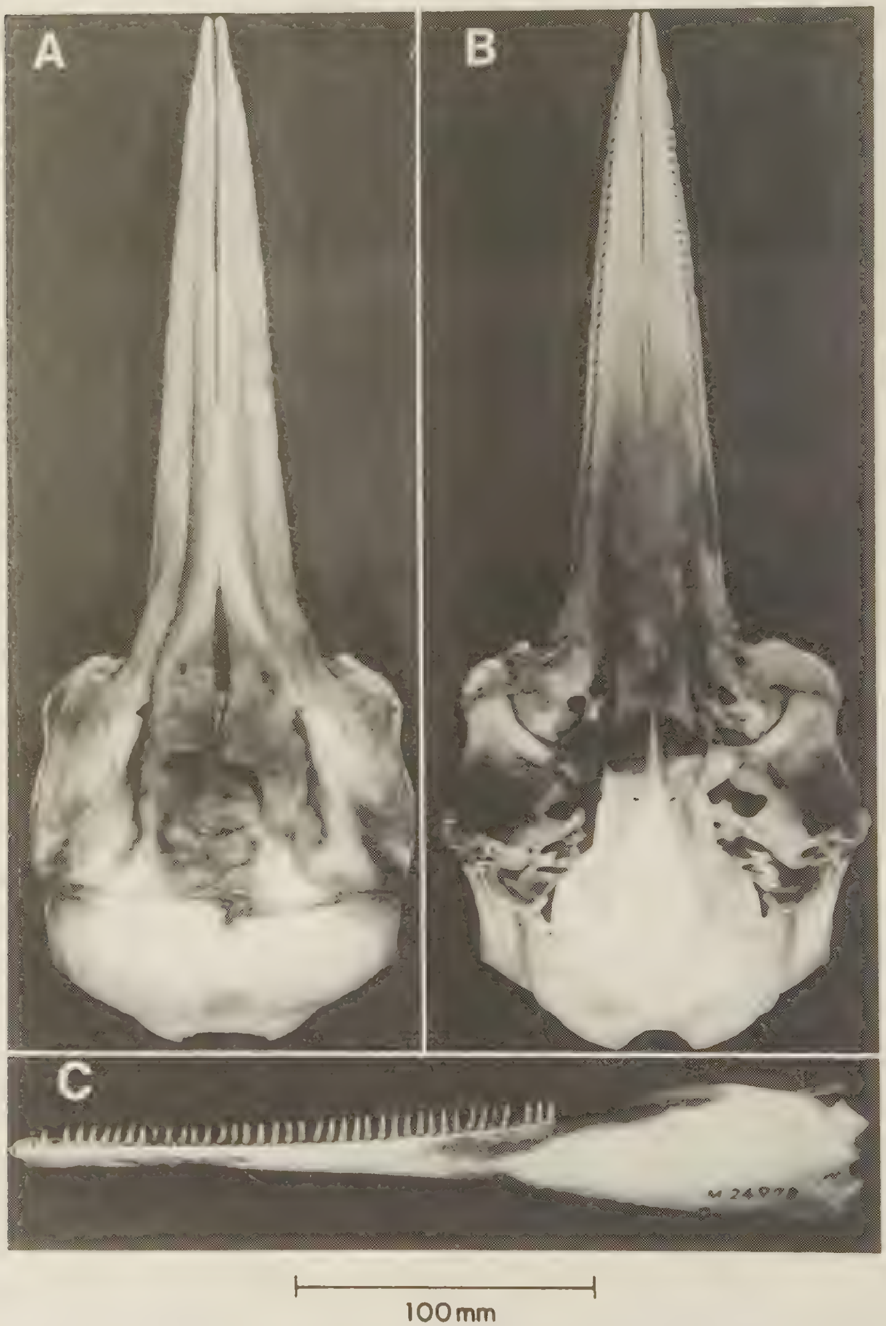
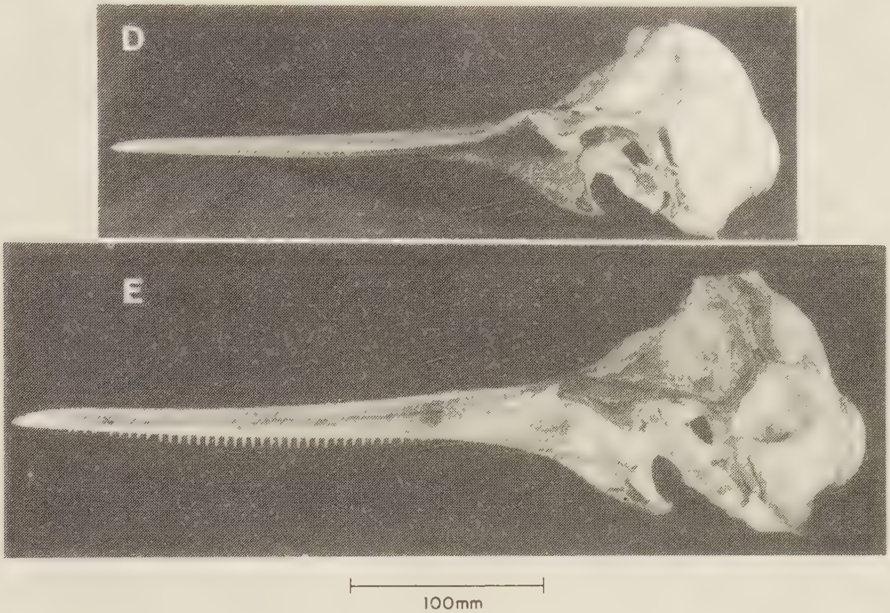


Figure 4. A, B, C, D: skull of dwarf spinner dolphin from the Gulf of Thailand (NSM M24978, physically male, 136 cm, condylobasal length 343 mm). E: lateral view of skull of spinner dolphin from the Atlantic coast of Florida (UF R-3-SLS, sexually adult female, 189 cm, condylobasal length 437 mm).



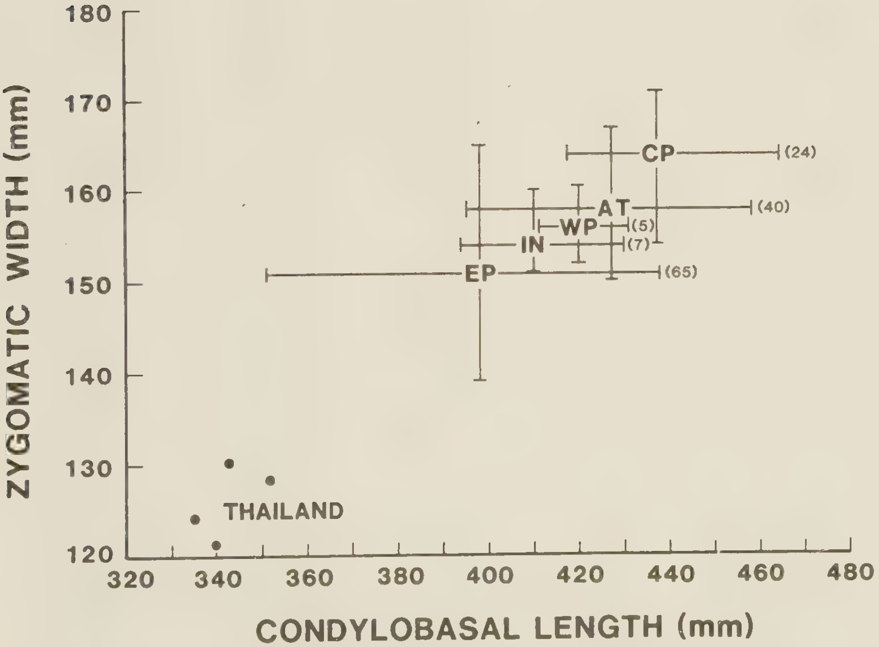


Figure 5. Comparison of adult skull length and width in Thailand specimens of *Stenella longirostris* with ranges and means for series from Indian Ocean (IN), western Pacific (WP), central Pacific (CP), eastern Pacific (EP; several populations pooled), and Atlantic (AT). See Table 2 for sources of data.

Table 2. Means, standard deviations (for sample sizes ≥30), sample sizes (in parentheses), and maximum and minimum values for selected skull measurements (cranially adult specimens only; in mm) and postcranial measurements (physically mature specimens only) for series of *Stenella longirostris* from the Gulf of Thailand and other regions. Data

	Thailand	Indian Ocean	Western Pacific
Condylobasal length	342.5	409.2	420.1
	(4) 335–352	(7) 394–430	(7) 411–431
Length of rostrum	219.8	264.9	272.1
	(4) 215–224	(7) 250–281	(7) 262–281
Width of rostrum at base	61.0	74.0	78.3
	(4) 57–66	(7) 71–76	(7) 73–84
Width of rostrum at ½ length	35.0	43.3	47.9
	(4) 33–37	(7) 42–45	(7) 44–54
Length of pmx's at ½ length	16.8	19.4	21.0
	(4) 15–18	(7) 18–20	(6) 19–23
Width of rostrum at ¾ length	25.0	31.0	31.4
	(4) 24–27	(7) 28–34	(5) 26–36
Greatest preorbital width	115.5	141.6	144.6
	(4) 111–120	(7) 135–146	(5) 140–150
Greatest postorbital width	128.3	155.4	160.8
	(4) 124–131	(7) 153–160	(6) 155–169
Greatest width of ext. nares	34.3	39.6	42.8
	(4) 33–36	(7) 38–42	(5) 40–45
Zygomatic width	125.8	154.0	156.2
	(4) 121–130	(7) 151–160	(5) 152–161
Greatest width of pmx's	52.3	61.4	62.2
	(4) 49–55	(7) 59–64	(5) 60–65
Parietal width	104.8	128.7	127.6
	(4) 103–108	(7) 122–133	(5) 125–131
Height of braincase	77.3	89.7	88.4
	(4) 76–78	(7) 88–95	(5) 86–93
Internal length of braincase	88.8	102.9	104.6
	(4) 81–92	(7) 100–106	(5) 102–108
Length of temporal fossa	45.8	50.0	47.4
	(4) 42–49	(7) 46–58	(5) 44–51
Height of temporal fossa	38.0	41.4	41.0
	(4) 36–40	(7) 39–45	(5) 36–44
Length of orbit	38.8	42.3	43.0
	(4) 38–40	(7) 40–44	(5) 40–46
Length of antorbital process	31.8	41.7	42.6
	(4) 30–34	(7) 40–45	(5) 39–47
Width of internal nares	34.8	42.0	44.6
	(4) 34–35	(7) 39–45	(5) 42–47
Length of upper toothrow	192.8	232.3	237.2
	(4) 185–198	(7) 224–242	(6) 219–246
Length of ramus	293.3	352.0	366.3
	(4) 287–303	(7) 336–370	(7) 360–371
Height of ramus	46.3	55.9	55.8
	(4) 45–47	(7) 55–57	(6) 55–57
Diameter of tooth (at midlength of lower row, transverse at alveolus)	3.00	—	3.00
	(3) 2.8–3.1		(2) 2.9–3.1

Table 2. Continued.

from Masaki and Kato (1979), Mizue *et al.* (1964), Mohan (1985), Ogawa (1936), Perrin (1975), Perrin *et al.* (1979, 1981), Robineau and Rose (1983), Ross (1984) and museum specimens listed in Materials and Methods.

Central Pacific	Eastern Pacific			Atlantic
	Costa Rican	Eastern	Whitebelly	
436.9 (24) 417–464	428.6 (5) 416–439	386.5 (26) 351–407	405.1 (25) 365–438	427.0 ± 13.10 (41) 395–458
282.6 (24) 263–304	279.0 (5) 269–288	245.5 (26) 218–262	258.0 (25) 227–278	276.8 ± 11.00 (41) 251–304
79.3 (24) 74–86	72.4 (5) 70–77	72.1 (29) 66–77	75.1 (28) 69–83	76.6 ± 3.41 (42) 68–83
47.0 (24) 42–56	42.0 (5) 39–43	41.6 (26) 37–47	42.6 (22) 39–51	44.4 ± 2.30 (41) 41–50
21.1 (24) 17–23	21.4 (5) 21–22	19.6 (26) 16–22	20.3 (23) 17–24	21.0 ± 2.32 (37) 17–32
32.3 (24) 27–37	29.8 (5) 28–32	30.5 (26) 26–36	31.9 (23) 29–36	31.9 ± 2.63 (39) 25–39
150.8 (24) 140–158	134.2 (5) 131–138	132.3 (29) 127–138	140.9 (28) 132–150	145.6 ± 3.86 (42) 137–153
165.2 (25) 158–172	151.2 (5) 149–152	148.1 (29) 140–154	156.7 (29) 148–167	161.1 ± 4.03 (41) 152–169
42.5 (25) 39–47	40.6 (5) 39–43	40.2 (29) 33–44	40.9 (29) 37–46	41.8 ± 1.63 (38) 38–45
163.5 (25) 154–171	150.4 (5) 149–152	146.4 (29) 139–153	155.5 (28) 145–165	159.2 ± 3.92 (40) 150–167
66.1 (24) 62–70	64.4 (5) 61–66	60.6 (29) 49–67	63.0 (29) 58–67	64.8 ± 2.38 (42) 60–71
131.4 (25) 122–140	128.8 (5) 127–130	125.9 (29) 119–132	130.2 (28) 120–139	130.5 ± 4.25 (41) 121–140
91.0 (24) 84–98	86.6 (5) 85–89	86.4 (29) 83–92	89.9 (28) 80–98	93.1 ± 3.94 (38) 85–107
105.5 (24) 100–110	99.8 (5) 97–103	100.0 (29) 95–108	103.7 (28) 94–113	106.4 ± 3.77 (37) 99–114
53.3 (25) 45–61	49.6 (5) 46–57	48.5 (29) 41–57	49.7 (28) 41–56	48.1 ± 3.30 (42) 42–56
42.9 (25) 37–50	36.4 (5) 34–42	36.6 (29) 29–47	40.6 (28) 32–46	38.3 ± 3.52 (42) 30–49
42.8 (25) 40–47	42.0 (5) 40–44	39.8 (29) 38–43	40.6 (29) 37–45	41.8 ± 2.10 (39) 39–50
44.7 (25) 40–49	42.6 (5) 41–45	39.9 (29) 33–45	40.9 (15) 35–45	43.4 ± 2.23 (39) 38–48
44.1 (25) 39–48	44.8 (5) 42–47	41.2 (29) 38–45	44.8 (29) 39–50	46.5 ± 2.26 (37) 42–53
245.6 (24) 224–263	245.0 (5) 238–255	212.2 (25) 192–229	224.0 (23) 192–246	243.5 ± 10.30 (41) 221–265
372.4 (23) 352–399	369.6 (5) 358–379	329.1 (27) 301–348	343.0 (29) 308–374	368.4 ± 11.68 (40) 343–399
58.4 (23) 53–64	55.2 (5) 53–57	52.3 (29) 47–57	54.7 (29) 50–60	56.4 ± 2.28 (41) 51–61
2.58 (23) 2.1–3.1	—	—	—	2.47 (29) 2.1–3.0

Table 2. Continued.

	Thailand	Indian Ocean	Western Pacific
Width of atlas	59 (1)	75.0 (2) 74–76	72 (1)
Height of atlas	35.0 (2) 33–37	46.0 (2) 46	46 (1)
Height of first lumbar	33.5 (2) 32–35	44.5 (2) 44–45	71 (1)
Width of first lumbar	122.5 (2) 120–125	174.0 (2) 163–185	169 (1)
Length of longest rib	184.0 (2) 180–188	251.0 (2) 234–268	262 (1)

minimum adult lengths for the very large eastern Pacific sample and the samples from other parts of the Indopacific and the Atlantic (Fig. 2, Table 1). (Minimum adult size was not available for the Australian series.) Four cranially adult males from Thailand were 129–137 cm long; two of these were physically mature, and all were below the minimum adult lengths of 142 cm for females and 144 cm for males given by Hembree (1986) for the northern Australian specimens. The Thailand sample is very small, however, and some overlap could be expected when larger samples become available. Four of the five females in the sample (94–133 cm) were cranially immature; the skull of a fifth female (141 cm) was too heavily damaged to allow estimation of maturity. The four adult males weighed 21.5–26.5 kg, far below the range of 47.7–76.7 kg for 20 adult males from the eastern Pacific (unpublished data, WFP) and 55.8–75 kg for 9 adult or maturing males from the Atlantic (Mead *et al.* 1980).

In other external dimensions (Table 1), the Thailand dolphins fell below the ranges of the series from the Indopacific, eastern Pacific and Atlantic in several anterior measures (tip of upper jaw to eye, to anterior insertion of flipper and to umbilical scar) but overlapped them in others, including dimensions of the appendages. Since the series did not overlap in total body length, this suggests that the appendages were on the average proportionately larger in the Thailand animals than in the others.

The maximum values of all dimensions for the northern Australian series fall outside the ranges for the Thailand animals, by several cm in most cases. (The minimum values for adults were not given by Hembree.) While, again, the Thailand sample is very small and overlap may be expected when more extensive and complete data become available, it is likely that the northern Australian form will prove to be larger on the average in several external dimensions in addition to total length.

The external photographs (Fig. 3) are not identified to specimen. They show the tripartite pattern typical of the species in the central and western Pacific, Atlantic and Indian Oceans, consisting of dark-gray dorsal cape, lighter-gray lateral field and a white underside (Perrin 1972, and 1975; Perrin *et al.* 1981). Thus, while small in size, the Thailand spinner does not resemble the small

Table 2. Continued.

Central Pacific	Eastern Pacific			Atlantic
	Costa Rican	Eastern	Whitebelly	
74.0	—	69.7	70.5	—
(3) 72–75		(6) 67–74	(8) 65–74	
44.0	—	43.0	43.3	—
(3) 43–45		(6) 40–47	(8) 40–46	
43.8	—	40.3	41.3	—
(3) 42–46		(6) 39–41	(7) 38–43	
181.0	—	166.0	166.8	—
(3) 177–184		(6) 162–171	(8) 162–171	
264.3	—	222.8	243.1	—
(3) 257–269		(6) 217–229	(8) 228–261	

eastern spinner of the eastern Pacific (152–199 cm for 1,128 adults; Perrin *et al.* 1985) in coloration; the latter is uniform gray with light patches in the genital and axillary regions (Perrin 1972). The eastern spinner also differs in shape of the dorsal fin, which is more erect than in the Thailand specimens (Perrin 1975).

Skull and skeleton—The Thailand spinner also has a very small skull (Fig. 4, 5); in condylobasal length, rostrum length, rostrum width at the base and at midlength, width of the premaxillae at rostrum midlength, width of external nares, length of the antorbital process, and length and height of the ramus, the four adult specimens overlap only the range for the eastern spinner (by 1–6 mm; Table 2). They fall below the ranges of zygomatic width, pre- and postorbital width, parietal width, height and length of the braincase, and width of the internal nares for all the series from the Indian Ocean, western Pacific, central Pacific, eastern Pacific (Costa Rican, eastern and whitebelly forms) and Atlantic. However, the Thailand skulls overlap all of the geographical series in length and height of the temporal fossa and length of the orbit. While the sample is very small, this suggests that the Thailand spinner skull differs in shape as well as size from those from other regions, with proportionately larger temporal fossae and orbits. For example, the ratio of the mean orbit length to mean condylobasal length is 0.113 as compared to the range for the other samples of 0.098 (central Pacific, Costa Rican and Atlantic) to 0.103 (Indian Ocean and eastern). In maximum premaxilla width, rostrum width at ¾ length, and length of the upper tooth row, the Thailand skulls overlap some of the other series as well as the eastern series, to a very slight extent. We did not have available to us skull measurements for the spinner dolphins collected from the gillnet fishery off northern Australia; judging from the distribution of body lengths (Fig. 2), these animals may also have small skulls.

The Thailand skulls have on the average about 5–8 fewer teeth per upper row and about 6–11 fewer per lower row than skulls in the other series (Table 3). In upper count, they overlap only the lower ends of the ranges for the eastern and Atlantic series (by 3 and 1, respectively); in lower count, they overlap slightly all but the small Costa Rican series.

The Thailand specimens are smaller than all of the other specimens in all of five postcranial dimensions (Table 2); the difference in length of the longest rib (a good index of girth) is especially striking.

The average total number of vertebrae in the seven skeletons available from Thailand is about 2–4 lower than in the other series. The range does not overlap that for the large eastern Pacific series. The difference appears to be mainly in the thoracics and lumbars. Nine Thailand specimens each have 14 thoracic vertebrae, whereas the averages for the other series range from 14.5 to 15.8. The caudal vertebrae and chevron bones are disarticulated for most of the specimens in all the series, precluding accurate determination of the beginning of the caudal series. However, placement of the first vertebra bearing a vertical foramen (on about vertebra number 46 on average in the Thailand series, versus 48–50 in the other series) indicates that there are probably fewer lumbars in the Thailand specimens than in the others.

Discussion

The Gulf of Thailand spinners may comprise a discrete breeding population, or they may be part of a large continuous population extending into other East Indian/Australasian waters. Larger samples may demonstrate more morphological congruence with the small spinners involved in the gillnet fishery in the Timor and Arafura Seas off northern Australia, or, if there is a single continuous population, a north/south cline in body size may exist. In any case, the northern Australian osteological specimens should be compared with larger samples from the Gulf of Thailand and, if possible, with material from localities between the two regions.

The question of population discreteness is not only important taxonomically but also has implications for conservation and management. If there is a separate population in the Gulf of Thailand, the impact of the shrimp fishery, if it is still operating, will be greater than would be the case were a more extensive population involved. Neither the size and status of the population nor the size and impact of the incidental kill can be estimated with existing data; the needed additional data should be collected (Perrin 1988).

The feeding ecology of the small spinners of this part of the Indopacific may be different than that of spinner dolphins in other parts of the world. Stomach contents of spinners from the eastern Pacific, Hawaii, India, and the Atlantic have contained primarily small mesopelagic fishes, squids and crustaceans (Perrin and Gilpatrick, in press). Spinner dolphins in Hawaii move offshore diurnally to feed on deep-living organisms that migrate toward the surface at night (Norris *et al.* 1985). However, the stomachs of dolphins captured in gillnets off northern Australia contained mainly reef-living and benthic organisms (Hembree 1986). The Gulf of Thailand dolphins were captured in demersal shrimp trawls and may also have been feeding on shallow-water benthic rather than mesopelagic animals (the entire Bight of Bangkok and most of the rest of the Gulf of Thailand is less than 50 m deep, Bartholomew 1958). This benthic feeding habit may be correlated with small size in the species.

Table 3. Means, standard deviations (for sample sizes ≥30), sample sizes (in parentheses), and maximum and minimum values for selected meristic characters for series of *Stenella longirostris* from Thailand and other regions. See Table 2 for data sources.

	Upp. teeth (per row)	Low. teeth (per row)	Total vertebrae	Thoracic vertebrae	First vert. foramen on #
Thailand	46.3 (9) 43–48	45.0 (8) 42–49	69.7 (7) 69–71	14.0 (9) 14	45.8 (9) 43–48
Indian Ocean	52.9 (15) 49–59	50.6 (15) 45–58	72.0 (5) 71–73	15.0 (4) 15	49.0 (4) 48–50
W. Pacific	53.3 (12) 48–61	51.4 (14) 47–60	72.2 (10) 71–75	14.8 (10) 14–16	48.0 (1)
C. Pacific	55.0 (29) 50–62	52.5 (29) 48–57	71.8 (9) 69–75	14.5 (10) 14–15	48.3 (11) 47–50
E. Pacific:					
Costa Rican	55.3 (5) 50–59	56.3 (5) 51–59	—	—	—
Eastern	52.6 ± 3.18 (32) 46–61	50.5 ± 2.39 (37) 45–56	74.3 (13) 73–76	15.4 (15) 14–17	50.3 (16) 47–54
Whitebelly	52.9 ± 2.51 (30) 49–59	51.3 ± 2.91 (32) 44–59	73.9 ± 1.27 (35) 72–77	15.8 ± 0.60 (34) 14–17	49.9 (20) 48–53
Atlantic	55.4 ± 3.01 (41) 48–64	53.9 ± 3.32 (43) 47–62	71.7 (27) 69–75	14.6 (26) 13–16	49.7 (6) 47–52

Average water temperatures to which the spinner dolphins in the shallow Gulf of Thailand are exposed could be expected to be generally higher than those to which mesopelagically feeding spinner dolphins in other regions are exposed. The proportionately larger appendages and the overall smaller size of the Thailand animals may be a manifestation of the general pattern recognized in "Allen's rule," *i.e.*, greater surface-to-volume ratios in warmer environments.

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8957

ARTIFICIAL REEFS: NOTHING MORE THAN BENTHIC FISH AGGREGATORS

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ABSTRACT

The potential for artificial reefs to substantially increase standing stock of marine resources is considered. Three sources—the Japanese artificial reef program; relationships between fishery production and the area of natural habitat for several fisheries; and population dynamics—offer evidence that artificial reefs do not substantially increase the standing stock of marine resources.

RESUMEN

Se considera el potencial de los arrecifes artificiales para aumentar sustancialmente el stock disponible de los recursos marinos. Tres fuentes de evidencia: el programa de arrecifes artificiales japonés, la relación entre producción y área del hábitat natural de varias pesquerías, y la dinámica de poblaciones, indican que los sustratos artificiales no aumentan sustancialmente el stock disponible de los recursos marinos.

DISCUSSION

Artificial reefs can be excellent fish aggregators, but they do not effectively increase standing stock. This position will be supported with three types of evidence: first, with observations from the Japanese artificial reef program; second, from the relationship between habitat and fishery production; and finally from considerations of population dynamics.

Between 1976 and 1987, the Japanese spent U.S. \$4.2 billion to construct and deploy 6,443 artificial reefs, covering 9.3% of the ocean bottom from shore to a depth of 200 m (Yamane, in press). But despite this enormous volume of artificial reefs deployed in coastal water, there has not been any measurable increase in coastal fishery landings (Japan: Statistics and Information Department 1984). Studies specifically investigating the impact of the artificial reefs have generally not documented any significant increases in fish production that can be attributed to the reefs (Kawasaki 1984; Kakimoto and Okubo 1985). After three visits to Japan and numerous discussions with people involved in all aspects of the Japanese artificial reef program, I believe the real benefit of the reefs is that they aggregate wide-ranging fishes close to shore so they can be harvested by fishermen with small vessels and thus keep the fleet of small vessels economically viable.

Outside of Japan, artificial reefs have not been deployed on a large enough scale to evaluate their effectiveness in increasing standing stocks. However, examining the relationship between habitat and fishery production can provide estimates of the level of fishery yield per area of habitat that might be expected from appropriately designed and sited artificial reefs. One example is penaeid shrimp: worldwide fishery yields range from 8 to 200 kg/hectare of intertidal nursery habitat (Turner 1977). In the case of artificial reefs, yields are measured in production per unit of reef volume. Thus if a square meter of intertidal habitat is assumed to also contain about a meter of vertical structure, grass, or mangrove, then these yield figures are equivalent to 0–0.02 kg/m^2. Another example is the coral reef systems, from which fishery yields have been reported in the range of 5–20 t/km^2 (Marten and Polovina 1982). If one square meter of coral reef habitat is conservatively assumed to be equal to one cubic meter of reef volume, then production per volume of reef habitat is 0.005–0.02 kg/m^3.

To put this production-per-unit-of-habitat volume in perspective, I will relate it to an example from California, where recent annual commercial landings for rockfishes are about 15,000 metric tons (MT) (California Department of Fish and Game 1987). I will assume that the average figure for fishery production per habitat volume from coral reef fisheries, 0.01 kg/m^3, can be applied to rockfishes. I will further assume that artificial reefs can be ten times more effective than natural habitat that might include barren or unproductive areas. With a level of fishery production of 0.1 kg/m^3 of habitat volume, it would require 15 million m^3 of artificial reefs to increase the annual rockfish catches by 10%. At the extremely low cost of \$10/m^3 of reef for construction and deployment, this would cost \$150 million. To put 15 million m^3 of artificial reefs into perspective, consider a space 100 × 50 m, about the size of a football field, covered with 1-m cubes. One such field would contain 5,000 m^3; therefore, 3,000 such fields covered with 1-m cubes would equal 15 million m^3. Of course the major flaw in this brute force approach to fishery enhancement is that even if this enormous volume of artificial reefs was built and deployed, any benefits would not be noticeable, because landings annually fluctuate by 10% to 20%. That is exactly one of the lessons the Japanese learned with their $4.2 billion experiment.

There is also the question of which resources lose habitat when low-relief habitat is covered with artificial reefs. There is a perception that low-relief habitat is not used by important commerical species, whereas high-relief habitat is preferred by valuable species. This is often based on the observation that the adults are seen and caught in high-relief habitat. This has been commonly accepted in Hawaii, but recently, when correct sampling gear was used, the juvenile habitat of the very valuable deepwater snappers was found to be the low-relief, flat-bottomed, sandy habitat, which had been considered a biological desert. Large-scale deployment of artificial reefs on this flat, sandy-bottom habitat would have attracted shallow-water reef fishes at the cost of destroying juvenile habitat for the more commercially valuable deepwater snappers. In Japan, a study around an artificial reef site found that the artificial reef attracted some species and repelled others and that the effectiveness of the reef could be negative, depending on which species were attracted or repelled (Kawasaki 1984).

The wide ranges in the levels of fishery production per area of habitat suggest that, although habitat is necessary, it is not limiting to production. Current research suggests that for many species, population size is determined during the larval rather than benthic phase. For example, the adult population of the Caribbean coral reef fish, *Thalassoma bifasciatum*, is determined primarily by recruitment and not by the supply of space on the reef (Victor 1983). In another study, the survival of juvenile reef fishes was estimated for varying levels of recruitment, and survivorship appeared constant — independent of juvenile density on the reef (Sale and Ferrell 1988). These studies indicate that even for coral reef fishes that require reef habitat during juvenile and adult phases, more reef habitat would not increase standing stock.

Insight into whether a resource can be enhanced with artificial reefs can be obtained from the relationship between larval settement density and fishery catches. If the relationship is linear, then the same percentage of the larval settlement is caught by the fishery, independent of density. However, if the fraction of the settled larvae, which ultimately contribute to the fishery, declines as the density of settled larvae increases, then density dependence may be a factor, and artificial reefs, which provide additional habitat and reduce the density at some stage, may increase fishery production. A relationship between larval settlement and fishery catches is available for a spiny lobster (*Panulirus cygnus*) fishery in western Australia (Phillips 1986). This relationship is linear, indicating that the same fraction of the settled larvae are captured as adults by the fishery, independent of the level of larval settlement. Thus, even for a spiny lobster which requires shelter, larval settlement is the limiting factor to production, and even at high postlarval densities, habitat is not limiting to fishery production.

Artificial reefs are often suggested as a solution to overfishing. Yet they do not help if either growth or recruitment overfishing is occurring. In the case of growth overfishing, they may aggregate younger fish, making them more vulnerable to capture and actually increasing overfishing. In the case of recruitment overfishing, standing stock is a fraction of its unexploited level, and habitat is certainly not limiting. Aggregating adults further simply increases catchability, and hence fishing mortality, which further reduces the spawning stock biomass.

Reefs are popular as management options because they do not require reductions in fishing effort and they aggregate fish, resulting in higher catches in the initial stages. Thus artificial reefs may actually be detrimental to the fishery and the stock simply because they allow managers to delay making hard but necessary decisions, such as imposing size limits or reducing effort.

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8958

Part III

SHOULD ANYONE BUILD REEFS?

Jeffrey J. Polovina

Clearly my two distinguished panelists have fallen under the seductive spell of artificial reefs and are unable to view them objectively as just one of many fishery management tools. I can sympathize with them. Many of us here have built an artificial reef on a barren ocean bottom to evaluate them for fishery management. When the site is revisited later, it is supporting a thriving marine community. It is easy to feel a rush of satisfaction observing the life created at the reef. It is difficult to resist the strong desire to further evaluate the effects of different designs, more holes, more height, different materials, different spacings, and so on. We probably all know colleagues, not ourselves of course, who are so caught up in evaluating reef designs that they have lost sight of the reason for building the reefs: to evaluate them as a tool for fishery management. These people cannot pass a scrap yard without looking for reef building materials; their pulse rate skyrockets when they look at catalogues full of pictures of Japanese artificial reef modules. However, to objectively evaluate artificial reefs, it is necessary to look at the fishery rather than just at the artificial reef site. We need to consider artificial reefs as just another management tool along with minimum sizes, closed seasons, catch limits, limited entry, closed areas, effort or gear restriction, and protection and restoration of natural habitat. When we do this, it becomes apparent that, relative to other management tools, artificial reefs are generally inefficient and, at worst, counterproductive and expensive.

Most fishery managers in the United States will tell you that the biggest problem they face is prevention of, or more often recovery from, overfishing. Often it is when catches have fallen due to overfishing that people clamor for artificial reefs. Unfortunately, they are not the appropriate tool to solve this or most other problems facing United States fisheries. As an example, let's take the case of overfishing. There are two types of overfishing: growth overfishing and recruitment overfishing. In the case of growth overfishing, the maximum yield of a fishery for a given level of fishing effort is not achieved because the fish being harvested are too small. Often the correct choice of a minimum size increases the landing weight by at least 10%, and the only cost is the salary of a few enforcement agents. Even assuming artificial reefs can actually increase fishery production, for artificial reefs to increase landings of the east coast snapper fishery, for example, by 10% requires that artificial reefs equivalent to 10% of the most productive natural habitat be deployed. This would be prohibitively expensive and inefficient. At worst, artificial reefs may cause young fish below the optimum size of harvest to be vulnerable to fishing gear and, hence, increase growth overfishing. This appears to be the case with tunas caught around fish aggregating devices. Clearly artificial reefs are an inappropriate tool to solve growth overfishing, yet they are commonly proposed and used in this situation instead of the less popular but more effective strategy of managing size at entry and fishing effort.

Recruitment overfishing, the other type of overfishing, occurs when the spawning stock biomass has been overfished and the stock is at low levels as a result of reduced larval recruitment. Here the tools managers need involve limiting fishing effort and/or protecting and replenishing the spawning stock. When the stock has been substantially reduced, habitat certainly is not limiting. Recall that the natural habitat supported a much larger pre-exploitation biomass. When a stock is fished at its maximum sustainable yield (MSY) level, the biomass may be about 50% of its pre-exploitation biomass, and when recruitment overfishing occurs, the stock may be further reduced to ≤25% of the pre-exploitation biomass. As long as habitat has not been greatly reduced, even at MSY and more so when recruitment overfishing occurs, there is plenty of habitat per fish, and additional habitat in the form of artificial reefs is totally unnecessary. Again, artificial reefs are inappropriate as a tool to solve recruitment overfishing and yet are frequently proposed instead of less popular effort restrictions. It is amazing that when fish stocks are overfished and not enough fish occupy all the natural habitat, people spend money to dump more habitat into the ocean and argue about how expensive the material should be and whether to use volunteers or pay fishery biologists.

Some fishery managers take the view that just by aggregating fishes, artificial reefs are helping the fishermen. If the stocks are already overfished, aggregation will result in lower equilibrium catches. The reason is that aggregation increases catchability which increases fishing mortality even if fishing effort does not increase. But frequently, artificial reefs also result in a shift in fishing effort from the natural habitat, where stocks are less aggregated to the artificial reefs, where stocks are more highly aggregated. This additional effort, targeting aggregated fishes, where catchability is higher, further increases fishing mortality. This increase in fishing mortality due to the artificial reefs moves the fishery further along the descending limb of the production curve to lower catches.

Some biologists assume that, if it is shown that artificial reefs actually increase fishery production, that alone is sufficient to justify their use. Their assumption, of course, is wrong. Not even demonstrating the cost effectiveness of artificial reefs is sufficient to justify their use. It must be shown that, relative to other management tools, artificial reefs represent the best long-term management strategy.

I challenge you to look at all the papers that promote the benefits of artificial reef in this conference and ask: Are they just a short-term fix or really beneficial in the long-term? Can the same result be achieved more efficiently with a management tool other than artificial reefs?

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8959

Density Dependence in Spiny Lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands

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Polovina, J. J. 1989. Density dependence in spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands. Can. J. Fish. Aquat. Sci. 46: 660–665.

A positive linear relationship between the ratio of natural mortality to von Bertalanffy growth and catch per unit effort (CPUE) and a negative relationship between asymptotic length and CPUE were observed for the spiny lobster, *Panulirus marginatus*, among seven banks in the Northwestern Hawaiian Islands prior to the development of a fishery (1977–81). Resampling two of these banks in 1986–87 after heavy fishing indicated an increase in the asymptotic length and a decrease in the length at onset of egg production.

Il existait une relation linéraire positive entre le ratio de la mortalité naturelle à la croissance von Bertalanffy et la prise par unité d'effort (PUE) ainsi qu'une relation négative entre la longueur asymptotique et la PUE chez la langouste, *Panulirus marginatus*, dans sept bancs de la partie nord-ouest de l'archipel hawaïen avant l'établissement d'une pêcherie (1977–81). Un nouvel échantillonnage de ces bancs en 1986–87, après une pêche intense, a indiqué un accroissement de la longueur asymptotique et une diminution de la longueur au moment de la production d'oeufs.

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Density-dependent relationships affecting growth, natural mortality, asymptotic size, and size at onset of sexual maturity in some lobster stocks have been difficult to rigorously document because of limitations in data bases and analytic methods (Chittleborough 1979; Morgan 1980; Munro 1983; Addison 1986). However, documenting these relationships is frequently cited as research critical to understanding lobster population dynamics (e.g. Cobb 1986). Addison (1986) hypothesized that, if a significant relationship between density and population parameters exists as a result of the lobster's use of shelters, management measures derived from changes in size-frequency distributions and standard yield-per-recruit models may be incorrect since they assume population parameters do not change with density.

Density-dependent relationships are examined for population parameters of the spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands (NWHI), a chain of small islands, banks, and reefs on the northwestern portion of the Hawaiian Archipelago (Fig. 1). Based on research sampling data from 1977 to 1981, estimates of density, in terms of catch per unit effort (CPUE); asymptotic length (L_∞); and the ratio of natural mortality to growth (M/K) for the spiny lobster are determined for seven NWHI banks prior to the development of a commercial fishery. Nine years after this initial sampling, an annual research program was initiated to resample the spiny lobster populations at Necker Island and Maro Reef, both having experienced heavy commercial fishing and reductions in lobster density. The changes in density, measured as changes in CPUE, are compared with changes in total mortality to growth (Z/K), L_∞, and size at onset of egg production.

Analytic Methods

Catch Rates

Standardized lobster sampling was conducted in 1977–81 at 26 banks in the NWHI and again in 1986–87 at Necker Island and Maro Reef, the two most productive and heavily fished banks. Lobster habitat at each bank was partitioned into 0.01 nmi^2 quadrats, and a randomly selected subset of the quadrats was fished at 20–90 m depths with California wire mesh, two-chambered lobster pots. The percent of the 0.01 nmi^2 quadrats sampled ranged from 60 to 90%; typically a greater proportion of the habitat was sampled at the smaller banks. At least eight strings of eight traps per string were baited and set overnight in each quadrat sampled. The trapped lobsters were measured and released at the trapping site. For each quadrat, the CPUE was computed as the number of lobsters trapped divided by the number of traps recovered. The bank CPUE and standard error were computed as the mean and standard error of the CPUE's from all the quadrats sampled.

The research sampling covered all seasons and at some banks extended for several years. However, neither seasonal factors nor trap selectivity appear to bias the trap data. Specifically, in a study on selectivity of traps as population sampling gear, MacDonald and Stimson (1980) compared lobster catch rates and size structure between trap and diver catches and observations at Kure Atoll in the NWHI. Their study concluded that (i) trap CPUE does not seem to be influenced by seasonal or lunar factors, (ii) trap catches do not appear to be influenced by a dominance hierarchy based on size, (iii) size distributions

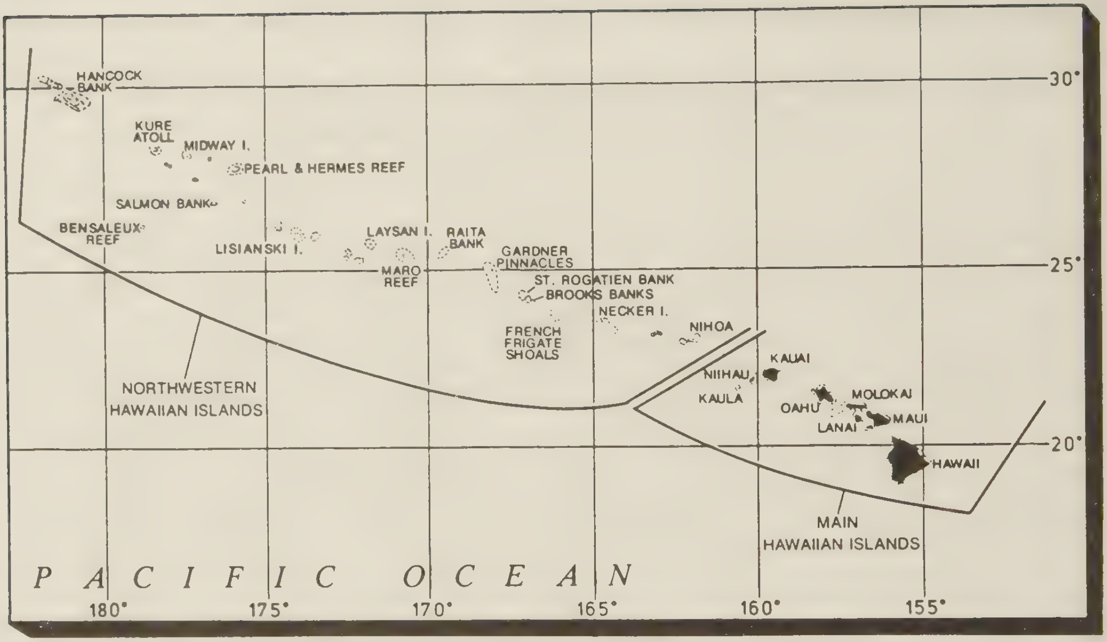

FIG. 1. The Hawaiian Archipelago, including the Northwestern Hawaiian Islands.

TABLE 1. Estimates of mean M/K, L_∞, and catch per unit effort (CPUE) (SE in parentheses) for lobster populations at seven banks in the Northwestern Hawaiian Islands. N denotes sample size.

Bank	Year	N	Mean CPUE	Mean L_∞	Mean M/K
Necker Island	1977	6474	5.76 (0.75)	113.8 (1.3)	4.22 (0.27)
Gardner Pinnacles	1977–80	390	1.68 (0.41)	115.0 (2.1)	2.20 (0.51)
Raita Bank	1977–80	384	1.13 (0.36)	128.1 (1.7)	1.56 (0.44)
Maro Reef	1977	2318	3.89 (0.45)	127.1 (1.9)	3.56 (0.30)
Laysan Island	1977	954	1.79 (0.39)	125.1 (2.5)	2.72 (0.49)
Pearl and Hermes Reef	1977–79	543	0.63 (0.20)	137.0 (2.2)	2.17 (0.39)
Midway	1977–79	896	1.48 (0.51)	117.2 (1.9)	2.55 (0.48)

of trap and diver-caught lobsters above about 85 mm carapace length show no difference, and (iv) trap CPUE appears to be a reliable measure of adult density.

Mortality to Growth Ratio and Asymptotic Length

Estimates of mortality and growth were computed as a ratio rather than separately because a recently developed estimator using length-frequency data permits estimates of this ratio that are more precise than if either parameter is determined separately (Wetherall et al. 1987). If growth and natural mortality vary with density, it will likely be a positive density and mortality relationship and an inverse density and growth relationship (Cobb and Phillips 1980). The ratio of mortality to growth is sensitive to both these relationships.

Although lobsters grow incrementally rather than continuously, the von Bertalanffy growth curve with parameters K and L_∞ adequately approximates a lobster growth curve (Morgan 1980). In the absence of fishing mortality under the assumptions of von Bertalanffy growth and a constant natural mortality rate (M) for lobsters above the smallest length fully represented in the catch (L_c), the length-frequency data can be used to estimate the ratio of instantaneous natural mortality to growth (M/K), with a relationship derived from the equation (Beverton and Holt 1957)

$$M/K = (L_\infty - \bar{l})/(\bar{l} - L_c),$$

where $\bar{l}$ is the mean length of all lobsters greater than L_c. Rearranging this equation to express $\bar{l}$ as a linear function of L_c gives

$$\bar{l} = L_\infty/((M/K) + 1) + L_c(M/K)/((M/K) + 1).$$

Now instead of treating L_c as a single value, a sequence of L_c and corresponding $\bar{l}$ values is constructed by beginning with the smallest L_c fully represented in the catch and increasing it in a regular fashion to the largest fish in the sample and computing an $\bar{l}$ for each. In practice, the lower limit of the first size class after the mode of the length-frequency distribution is used as the first L_c value, and each subsequent L_c value is taken as the lower limit of each progressively larger size class. Regressing the sequence of $\bar{l}$ values on the corresponding L_c values (weighted by the standard errors of $\bar{l}$) gives estimates of the slope and intercept of equation (1), which can be solved for L_∞ and M/K (Wetherall et al. 1987). When fishing mortality (F) is

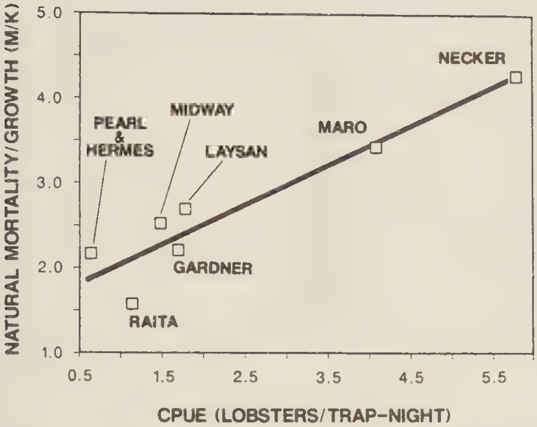

FIG. 2. Plot of the ratio of natural mortality to growth (M/K) against catch per unit effort (CPUE) for seven banks in the Northwestern Hawaiian Islands. The line is the regression equation $M/K = 1.63 + 0.46 \cdot \text{CPUE}$.

TABLE 2. Estimates of mean catch per unit effort (CPUE), Z/K, and L_∞ (SE in parentheses) for lobster populations at Necker Island and Maro Reef in 1986–87. N denotes sample size.

Location	N	Mean CPUE	Mean L_∞	Mean Z/K
Necker Island	2106	2.14 (1.24)	158.2 (5.3)	6.28 (0.57)
Maro Reef	2351	2.65 (0.67)	132.7 (0.63)	3.16 (0.10)

present, this method estimates the ratio of total mortality ($Z = M + F$) to growth (Z/K) and L_∞.

Because of differences in the length-frequency distributions between males and females, estimates of M/K and L_∞ were first computed for males and females separately, then averaged for a mean bank estimate.

Length at Onset of Egg Production

The research sampling recorded whether females were carrying external eggs. A function of the hyperbolic tangent (Tanh) is fit to the proportion of females with eggs (Y), where carapace length class (X) is the independent variable and parameters A, B, and C are estimated with the model

$$Y = A(1 + \text{Tanh}[B(X-C)]).$$

A weighted least squares estimation is used, where the weights are the number of females in the length class. The parameter C is the carapace length, where the percent of the females with eggs equals one-half the asymptotic level ($2A$), and this is taken as the estimate of length at onset of egg production (L_m).

Results

Although 26 banks were sampled in the NWHI for spiny lobsters (Uchida and Tagami 1984), only seven banks met the minimum sample size requirement based on a simulation analysis with the M/K and L_∞ estimation procedure (see Wetherall et al. 1987). Thus, the analyses used only the seven banks where size-frequency samples of at least 150 lobsters were measured for each sex, from a period prior to any significant fishing effort. Estimates of mean M/K, L_∞, and CPUE for each of the seven banks are in Table 1. A regression of mean bank M/K estimates on mean bank CPUE shows a significant positive relationship ($P<0.001$, $R^2 = 0.88$; Fig. 2). Lobsters at banks with high CPUE have significantly higher natural mortality or lower growth or both than at banks with low CPUE.

A regression of L_∞ on mean CPUE suggests that these variables are negatively correlated, but the result is not statistically significant ($P = 0.27$). However, simulation studies show that the estimates of L_∞ can be negatively biased for small sample sizes (Wetherall et al. 1987). When L_∞ is regressed on CPUE with a weighted regression where the weights correspond to the sample size of lobsters measured at each bank, the coefficient of CPUE is estimated as -2.6, which is statistically significant ($P = 0.08$) and indicates L_∞ varies inversely with CPUE.

Necker Island and Maro Reef experienced considerable fishing effort after 1980; the greatest decline in CPUE occurred at Necker Island, which is closer to the fishing port in Honolulu and has a smaller area of productive habitat than Maro Reef. The 1986–87 mean CPUE's were 37 and 68% of their 1977 levels at Necker Island and Maro Reef, respectively (Table 1, 2). At Necker Island, the mean L_∞ was estimated at 158.2 mm for 1986–87 and at 113.8 mm prior to the fishery. The difference in L_∞ between the two periods is statistically significant ($P<0.05$) (Table 1, 2; Fig. 3). At Maro Reef, even though initially L_∞ was relatively large there was a statistically significant increase in L_∞ , although much less than that observed at Necker Island, after the reduction in CPUE ($P<0.05$) (Table 1, 2).

Although estimates of M/K are unavailable for Maro Reef and Necker Island for 1986–87, estimates of M/K for 1977 compared with estimates of Z/K for 1986–87 strongly suggest that M/K declined at both banks as CPUE declined. At Maro Reef, M/K for 1977 and Z/K for 1986–87 did not significantly differ. Because the 1986–87 CPUE is 68% of the 1977 level, fishing mortality must be substantial, and hence, M/K must have declined in 1986–87. At Necker Island, Z/K is greater than the 1977 M/K; however, if F/M is estimated as the difference between the 1986–87 Z/K and 1977 M/K divided by the 1977 M/K, an F/M estimate of 0.49 is obtained. This estimate very likely underestimates the ratio of fishing mortality to natural mortality, given that 1986–87 CPUE is 37% of the 1977 level.

Using the Beverton and Holt (1957) yield equation to estimate the reduction in population biomass of a stock relative to its unexploited level as a function of F/M (Beddington and Cooke 1983), when $M/K = 3$, the exploitable biomass will be reduced to 55 and 37% of the level prior to exploitation when $F/M = 0.5$ and 1.2, respectively. Thus, at Necker Island, the reduction of the 1986–87 CPUE to 37% of the unexploited level suggests F/M exceeded 1.0 and certainly the 0.49 estimated under the assumption that M/K is density independent. If F/M were 0.50, the 1986–87 CPUE would be expected to be about 50% of the 1977 level. The M/K, which corresponds to the 1986–87 CPUE level of 2.14, can be calculated from the equation derived from the regression of M/K on CPUE for the seven banks (Fig. 2). This equation estimates $M/K = 2.73$ at Necker Island in 1986–87. With this estimate of M/K and Z/K of 6.28, F/M is estimated to be 1.3, which is consistent with the estimate from the Beverton and Holt (1957) equation given the level at 1986–87 CPUE relative to 1977.

The percentage of females sampled with external eggs increased as a function of carapace length from zero to an asymptotic level (Fig. 4). By 1987, carapace lengths at onset of egg production at both Necker Island and Maro Reef were

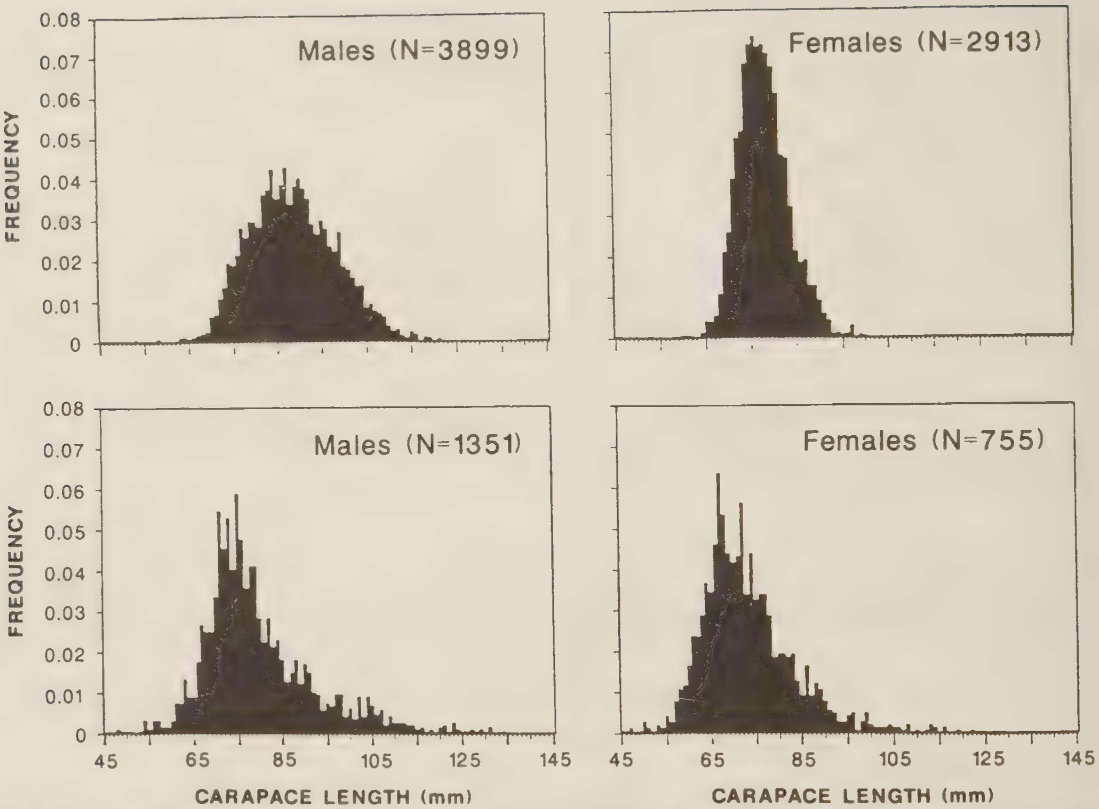

FIG. 3. Plots of length-frequency samples for male and female lobsters from Necker Island obtained from 1977 (top) and 1986–87 (below) sampling periods. (*N* denotes the number of lobsters in each sample.)

significantly lower than in 1977 ($P<0.05$) (Table 3). At Necker Island, the length declined from 67.8 mm in 1977 to 60.8 mm in 1987 (Table 3). At Maro Reef, the length declined from 74.8 mm in 1977 to 68.2 mm in 1987 (Table 3).

Discussion

A positive relationship has been shown to exist between M/K and CPUE over seven banks. The similarity in coral reef habitat and reef fauna between these banks (Grigg 1984; Hobson 1984), the evidence that trap catches are a reliable measure of adult abundance and size structure (MacDonald and Stimson 1980), and the indication that M/K decreases with CPUE at Necker Island and Maro Reef when density is reduced due to fishing — all argue that this relationship is likely not due to other factors, which might differ between banks, and further indicate a positive relationship between M/K and density. As to whether the change in the ratio of M to K is due to changes in M or changes in K or both, the separate estimates of the parameters needed to address that issue are not available. However, studies on other species of spiny lobsters suggest that it is likely that both M and K change with density. Munro (1983) estimated the natural mortality coefficient (M) for *P. argus* was 0.52 for an unexploited stock, 0.23 for a moderately exploited stock, and 0.14 for a heavily exploited stock. A similar relationship between density and natural mortality was indicated in *P. cygnus* (Cobb and Phillips 1980). Likewise, growth can be influenced by food and space availability, which change as density changes (Cobb and Phillips 1980).

The inverse relationship between L_∞ and CPUE, both between banks and over time at Necker Island and Maro Reef, is consistent with the hypothesis that asymptotic size changes inversely with density. Differences in the volume of shelters at two areas in England have been suggested as the cause of marked differences in the size structure of the lobster, *Homarus gammarus*, populations: the area where large shelters are abundant also has more large lobsters (Howard 1980). In the NWHI, the banks all have the same coral reef habitat, so it is unlikely that the size structure of the habitat differs between banks. However, when density is high, crowding may occur even in large shelters and effectively reduce shelter size.

Changes in the length at onset of maturity apparently due to changes in density have been observed in some fish populations. Shelton and Armstrong (1983) documented a 3-cm decline in the length at maturity of the South African pilchard, *Sardinops ocellata*, during a period of substantial population decline. By contrast, there was a 1-cm increase in the length at onset of sexual maturity in the South African anchovy, *Engraulis capensis*, after a period of population increase. Rothschild (1986) suggested that, when a population experiences a reduction in density, the increase in available food for each individual will result in an increase in the rate of sexual development and

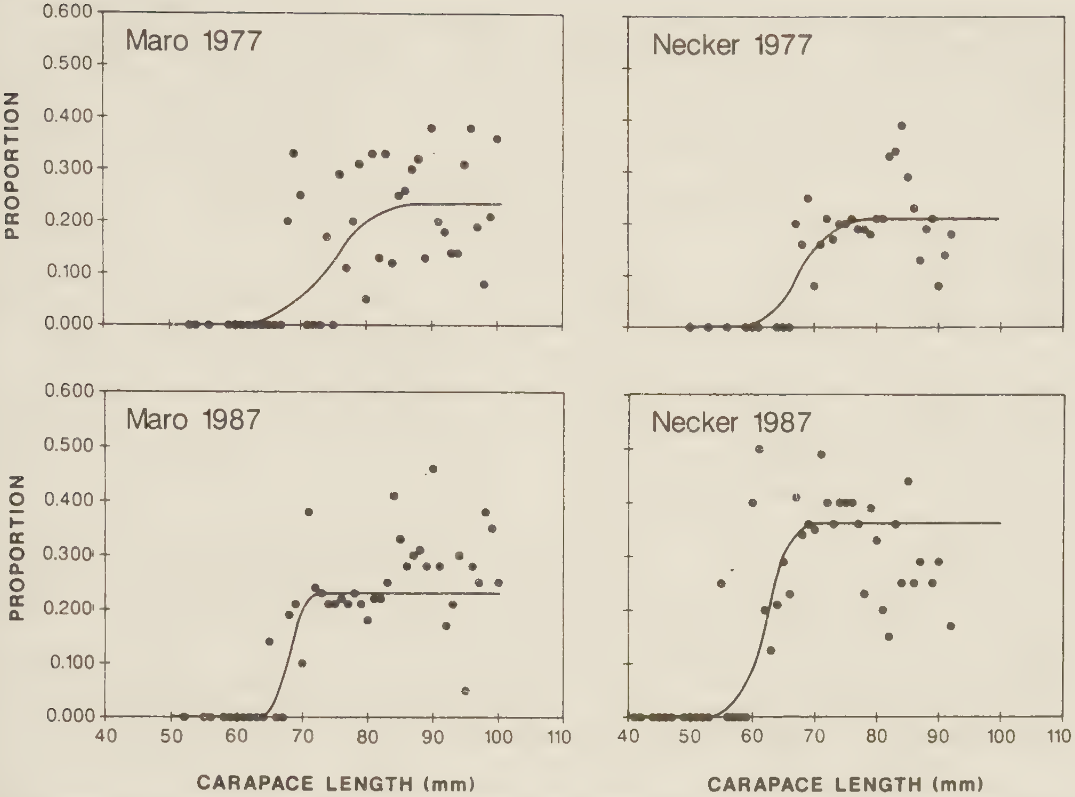

FIG. 4. Proportion of female spiny lobsters at Necker Island and Maro Reef with eggs as a function of carapace length for 1977 and 1987.

TABLE 3. Length at onset of egg production for 1977, 1985–86, and 1987. CL = carapace length (mm) (SE in parentheses), L_m/L_∞ = ratio of length at onset of egg production to female asymptotic length, and N denotes sample size.

	1977			1985–86			1987		
Location	N	CL	L_m/L_∞	N	CL	L_m/L_∞	N	CL	L_m/L_∞
Necker Island	1955	67.8 (1.5)	0.66	1491	57.9 (1.0)	0.41	797	60.8 (1.1)	0.47
Maro Reef	630	74.8 (2.5)	0.61	1614	70.5 (1.9)	0.59	873	68.2 (0.8)	0.54

hence an attainment of the onset of sexual maturity at a smaller size. However, it is also possible that behavioral interactions are important and smaller females are responding not just to a reduction in density but also to a reduction in number of larger females. The observed reductions in length of egg-bearing females at Necker Island and Maro Reef are consistent with both these hypotheses.

A hypothesis that the size at onset of egg production is determined exclusively by age has been used to explain differences in the size at onset of egg production for the rock lobster, *Jasus lalandii*, in different areas of the Benguela ecosystem (Beyers and Goosen 1987). It is argued that the differences in the size at onset of egg production result from differences in growth, so faster growing lobsters are larger when they reach the age at onset of sexual maturity. If the onset of egg production is determined exclusively by age and if growth increases when density is reduced by fishing, then the size at the onset of egg production should increase as fishing increases and not decrease as observed in the NWHI. An explanation for the difference between this hypothesis and the NWHI findings is that the NWHI fishery only harvests lobsters above the size at onset of egg production; hence, there is no reduction in juvenile lobsters and perhaps no increase in juvenile lobster growth, even though total lobster density decreases.

A management implication of the finding that M/K and L_∞ vary with density is that the application of static yield-per-recruit models can be misleading. Suppose managers want to determine the minimum length at which spiny lobsters should be harvested to maximize the yield-per-recruit at Necker Island when F/M is at 1.3 (estimated 1986–87 level). The Beverton and Holt (1957) yield-per-recruit model can be formulated in terms of M/K, Lr/L_∞, and F/M, where Lr is the length at entry to the fishery (Beverton and Holt 1966). If this model is used with the 1977 data ($M/K = 4.22$; $L_\infty = 114$ mm), the minimum length to maximize yield-per-recruit will be set at 41 mm. However, based on the estimated values of M/K and L_∞ (M/K

estimated from the M/K versus CPUE regression) in 1986–87, the minimum length should be 67 mm. The fishery operating with a minimum length of 41 mm will have a yield-per-recruit that is 20% lower than the maximum achieved with the 67 mm minimum length under the 1986–87 population parameters.

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8960

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IMPACTS OF ARTIFICIAL REEFS ON FISHERY PRODUCTION IN SHIMAMAKI, JAPAN

Jeffrey J. Polovina and Ichiro Sakai

ABSTRACT

The role of artificial reefs as a tool for increasing fishery production rather than just aggregating fish is addressed for two fisheries, octopus, *Octopus dofleini,* and flatfish, (Pleuronectidae), near Shimamaki, Japan. The time series of catch and effort data examined covers periods before and after two adjacent fishing grounds received 8,645 and 40,766 m^3 of artificial reef. Octopus catches were increased by 4% per 1,000 m^3 of artificial reef or by an average of 1.8 kg/m^3 of artificial reef. Artificial reefs aggregated flatfishes but did not increase catches in the regions. A survey of fishermen in the two regions revealed that the reefs generally are considered beneficial.

Artificial reefs are widely advocated as a tool to enhance fishing. The U.S. Congress established a national policy to promote the use of artificial reefs (Stone, 1985). Japan has a long history of artificial reef usage, and its government currently spends about US$10 million annually on the construction and deployment of artificial reefs in its coastal waters. The Japanese Government has justified this program with reports of annual combined pelagic and demersal catches at the reefs of up to 16–20 kg/m^3 of artificial reef (Sato, 1985). However, these catch rates do not measure the extent that artificial reefs increase fishery production in a region because, if the reefs were not present, many of these fishes might have been caught at the surrounding natural habitat instead. Evaluating the extent that artificial reefs can produce a sustainable increase in fishery production in a region, rather than just aggregate fish already present, is an important ecological question as well as a high priority research topic with important consequences for fisheries management (Bohnsack and Sutherland, 1985; Sato, 1985).

This study compares annual catches and catch per unit of effort (CPUE) between two adjacent fishing grounds. Examining two regions rather than just one separates the effects of artificial reefs on catches from the effects of year-class strength, changes in fishing power, and market factors. Any changes in relative catch and CPUE, corresponding to differences in the magnitude of artificial reefs between the two regions, are likely due to the artificial reefs. This study is believed to be the first to quantify the extent that artificial reefs produce a sustainable increase in fishery production.

METHODS

The two fishing grounds are located off the rural village of Shimamaki on the southwest side of the island of Hokkaido, Japan. The region's primary industry is fishing, and the fishing grounds, which lie offshore of a 27-km stretch of coastline, are divided into a 15-km stretch of coastline fished exclusively by the West Shimamaki Fishery Association, while the remainder is fished exclusively by the East Shimamaki Fishery Association. The two cooperatives are composed primarily of small (<10-ton) vessels fishing a variety of gear including hook and line, gill nets, and longlines. No large trawlers fish the area.

Commonly caught at, or near, the artificial reefs are the Pacific giant octopus, *Octopus dofleini* or mizudako, and a number of flatfishes (Pleuronectidae). For these two resources in East and West Shimamaki, a relatively long time series of catch data, and a shorter time series of CPUE data, are available.

The octopus has a rapid growth, attaining a weight of 15 kg in 3 years and reaching a maximum of 30 kg. Females become sexually mature after 3 years and, when spawning, deposit their eggs in

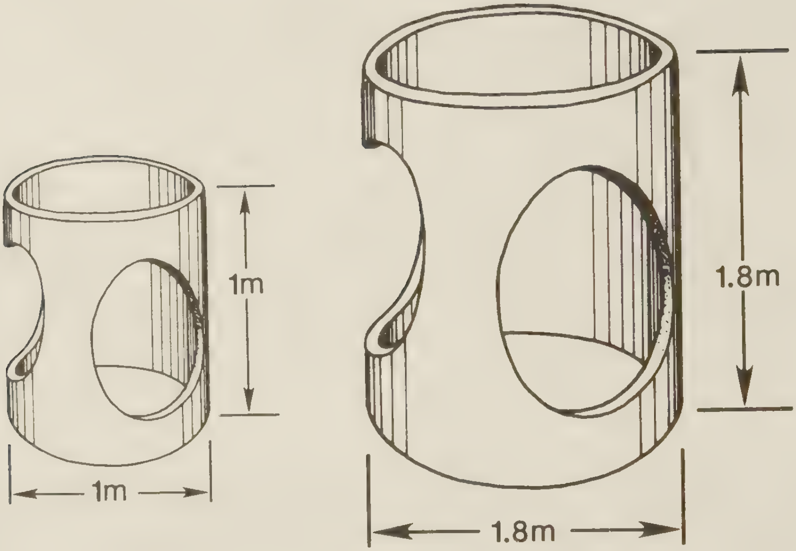


Figure 1. Small and large reef modules deployed in East and West Shimamaki.

rocky areas and guard them until hatching occurs. The larval state of this species apparently is short, after which the animals settle on benthic substrate. This species shows cryptic and solitary behavior, hiding in holes with one octopus per hole (Hartwick et al., 1978). The immature animals are fished at 40 to 60 m depths with octopus boxes or pots, which attract by offering shelter, whereas older animals are often caught with unbaited longlines. The fishery around Hokkaido has been stable since at least 1955 (Osako and Murata, 1983).

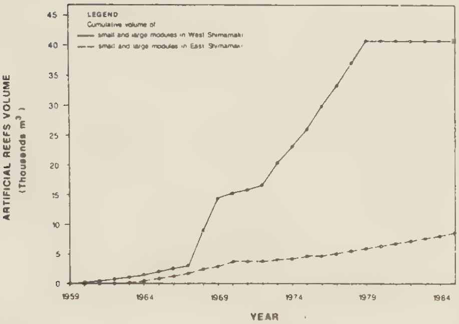
Of the flatfishes caught in the Shimamaki region, the most highly valued is the hirame or bastard halibut, *Paralichthys olivaceus*. Other flatfishes include the pointhead flounder, *Cleisthenes pinetorum herzenstein*; the smallmouth sole, *Limanda herzensteini*; and the flathead flounder, *Hippoglossoides dubius*. These fishes often are found on flat bottom areas; however, tracking studies with sonic tags show that, in areas with artificial reefs, the fish frequently move in and around the reefs perhaps to forage (Kakimoto, 1984). Flatfishes are fished with gill nets in the shallow (30–60 m) inshore waters of Shimamaki. The resource is heavily fished, and there is concern that growth overfishing is occurring.

The artificial reefs were composed of small (0.785 m^3 enclosed volume) or large (4.58 m^3 enclosed volume) cylindrical concrete modules with several large holes in the wall (Fig. 1). In West Shimamaki in 1960–1976, a total of 33,446 small modules were deployed in five locations 1–3 km offshore at depths of 30–40 m on either sand or gravel bottoms. The largest group had 5,000 modules, and the smallest, 555 modules. In 1976–1979, a total of 3,168 large modules were deployed over the same five locations, and at two new locations 1.5–3 km offshore at depths of 30–40 m on sand and gravel bottoms. West Shimamaki has a total of 36,614 artificial reef modules with an enclosed volume of 40,766 m^3 (Fig. 2).

In East Shimamaki in 1963–1975, 5,943 small modules were deployed at a single location 2.6 km offshore on a sandy bottom at a depth of 40 m. In 1977–1985 in the same location, 869 large modules were deployed. East Shimamaki has a total of 6,812 artificial reef modules with an enclosed volume of 8,645 m^3 (Fig. 2).

Aggregation and Enhancement Models.—The small area of the East and West Shimamaki fishing grounds makes it likely that recruitment for octopus and flatfishes comes from outside the region; hence, a linear relationship is assumed to exist between catch and fishing mortality in this area.

Any increase in catches and CPUE in the West, relative to the East, may be due to a net enhancement of the resources, or to movement between the two regions as a result of the greater reef volume in the West. To distinguish between these two possibilities, an enhancement model and an aggregation model are considered. The enhancement model hypothesizes that artificial reefs increase catches over those produced by the natural habitat in both regions, by an amount proportional to the artificial reef volume in each region. The aggregation model assumes that the combined catch from both regions does not



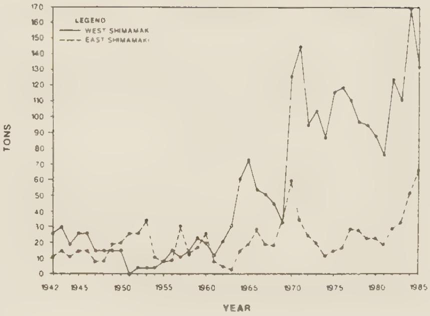


Figure 2. (Left) Cumulative volume of combined small and large module artificial reef volume for East and West Shimamaki.

Figure 3. (Right) Catches of octopus from East and West Shimamaki Fishery Associations from 1942 to 1985.

increase because of the artificial reef volume, and that a fraction of the combined catch moves from one region to the other in proportion to the difference in artificial reef volume between the two regions. The volume of artificial reefs typically has been used as a measure of their potential effectiveness, and it probably is a reasonably good index for the octopus found within the reef structure.

Specifically, let Cw(t) and Ce(t) denote the catches for a specific resource group in West and East Shimamaki, respectively, in year t. Let Fw(t) and Fe(t) denote fishing mortality, and Nw(t) and Ne(t) denote the fishable biomass associated with the natural habitat in the two regions, in year t. Let Rw(t) and Re(t) denote the cumulative artificial reef volume deployed up to and including year t in West and East Shimamaki, respectively.

For the enhancement model, we have

$$\mathrm{Cw}(t) = \mathrm{Fw}(t)\cdot\mathrm{Nw}(t)(1 + \mathrm{B}\cdot\mathrm{Rw}(t)) \tag{1}$$

and

$$\mathrm{Ce}(t) = \mathrm{Fe}(t)\cdot\mathrm{Ne}(t)(1 + \mathrm{B}\cdot\mathrm{Re}(t)), \tag{2}$$

where B is a constant such that 1 m³ of artificial reef volume increases the catch by 1 + B. From Equations (1) and (2), the ratio of catches and the ratio of the CPUE of West to East, by year, can be expressed as

$$\mathrm{Cw}(t)/\mathrm{Ce}(t) = (\mathrm{Fw}(t)\cdot\mathrm{Nw}(t))/(\mathrm{Fe}(t)\cdot\mathrm{Ne}(t))(1 + \mathrm{B}\cdot\mathrm{Rw}(t))/(1 + \mathrm{B}\cdot\mathrm{Re}(t)) \tag{3}$$

and

$$\mathrm{CPUEw}(t)/\mathrm{CPUEe}(t) = (\mathrm{qw}\cdot\mathrm{Nw}(t)/\mathrm{qe}\cdot\mathrm{Ne}(t))(1 + \mathrm{B}\cdot\mathrm{Rw}(t))/(1 + \mathrm{B}\cdot\mathrm{Re}(t)), \tag{4}$$

where qw and qe are the catchability coefficients in West and East Shimamaki, respectively.

Although there may be annual changes in fishing mortality, biomass, and catchability coefficients that are due to variation in year-class strength, changes in fishing effort, gear, and power and economic factors, the similarity between the two regions' environment and fishing fleets suggests that the ratios qw•Nw(t)/qe•Ne(t) and Fw(t)•Nw(t)/Fe(t)•Ne(t) will remain relatively constant over time. Under this assumption, the coefficient B can be estimated from Equation (3) or (4) with a nonlinear regression of Cw(t)/Ce(t) or CPUEw(t)/CPUEe(t) on Rw(t) and Re(t).

The aggregation model assumes that the reefs do not increase the abundance of the resource, but rather, move the resource between the two regions in proportion to the difference in the artificial reef volume:

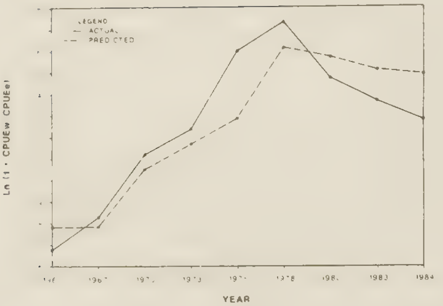
$$\mathrm{CPUEw}(t) = \mathrm{qw}\cdot\mathrm{Nw}(t)(1 + \mathrm{B}\cdot(\mathrm{Rw}(t) - \mathrm{Re}(t))), \tag{5}$$

$$\mathrm{CPUEe}(t) = \mathrm{qe}\cdot\mathrm{Ne}(t)(1 - \mathrm{B}\cdot(\mathrm{Rw}(t) - \mathrm{Re}(t))), \tag{6}$$

and

$$\mathrm{CPUEw}(t)/\mathrm{CPUEe}(t) = (\mathrm{qw}\cdot\mathrm{Nw}(t)/\mathrm{qe}\cdot\mathrm{Ne}(t))(1 + \mathrm{B}\cdot(\mathrm{Rw}(t) - \mathrm{Re}(t))/(1 - \mathrm{B}\cdot(\mathrm{Rw}(t) - \mathrm{Re}(t))). \tag{7}$$

The best way to distinguish between the aggregation and enhancement models is to examine CPUEw(t) − CPUEe(t). In the aggregation model, as the CPUE in one region increases, the CPUE in the other



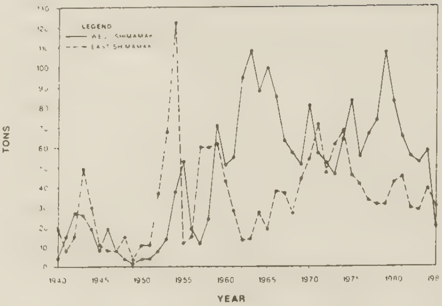


Figure 4. (Left) Actual and predicted values of Ln(1 + CPUEw/CPUEe) for octopus by year (predicted values from model y = 0.75(1 + 0.00004•RW)/(1 + 0.00004•RE)).

Figure 5. (Right) Catches of flatfishes in East and West Shimamaki Fishery Associations, 1940–1985.

region must decline; therefore, the difference increases faster as a function of reef volume than in either region alone. In the enhancement model, each region is affected independently of the other. Because the difference in CPUE's is affected by changes in year-class strength, the ratio of CPUEw(t) − CPUEe(t) divided by CPUEw(t) + CPUEe(t) regressed on Rw(t) − Re(t) is used to distinguish between the two models.

RESULTS

OCTOPUS. Octopus catch data from East and West Shimamaki were available from 1942 to 1985 (Fig. 3): Catches were similar from 1942 to about 1961, then began increasing in the West and, since about 1970, averaged about 5 times higher than in the East. Vessel tonnage of octopus fishing vessels in both regions had a similar constant rate of increase, roughly doubling in both associations. Estimates of vessel tonnage from 1965 to 1984 are used as a measure of annual fishing effort to compute a CPUE series, fit to the models developed in the previous section.

The ratios of the West to East CPUE's and catches were fit with nonlinear regression to the cumulative combined volume of large and small artificial reef cylinders (Equations (3) and (4)). The fit of the models was improved by using Ln(1 + CPUEw(t)/CPUEe(t)) and Ln(1 + Cw(t)/Ce(t)) as the dependent variable, instead of using simply the CPUE or catch ratios. Both regressions produced similar and statistically significant estimates of the parameter B, supporting the hypothesis that the artificial reefs increased the fishery production of octopus (Table 1, Fig. 4). The estimate of B (4.0×10^{-5}) from the CPUE regression is probably more accurate than from the catch regression (3.2×10^{-5}) because the CPUE regression, although based on a shorter time series, involves an effort measure. The estimates of the intercepts of Equations (3) and (4) (qw•Nw/qe•Ne and Fw•Nw/Fe•Ne) were not statistically different from 1.0 ($P > 0.10$). Further, the fit of these regressions was slightly better if the independent variable was the cumulative volume of only small modules rather than small and large combined, but the improvement was not significant ($P > 0.10$).

The ratio of CPUE's and difference of CPUE's divided by the sum of the CPUE's, under the assumptions of the enhancement and aggregation models (Equations (3), (4), (5), and (6)), were fit to the reef volume with the further assumption, previously tested, that qw•Nw/qe•Ne was 1.0 (Table 2). Under the aggregation model, when qw•Nw/qe•Ne is 1.0, the regression model is linear with the dependent variable (Rw(t) − (Re(t)) and, under the enhancement model, is

Table 1. Fit of enhancement model to catch and catch per unit effort (CPUE) data with estimates of parameter B for octopus and flatfishes

Dependent variable	Species	B	SE	R^2
Ln[1 + (CPUEw/CPUEe)]	Octopus	4.0×10^{-5}	1.9×10^{-5}	0.73
Ln[1 + (Cw/Ce)]	Octopus	3.2×10^{-5}	1.1×10^{-5}	0.30
Ln[1 + (CPUEw/CPUEe)]	Flatfishes	1.4×10^{-5}	1.6×10^{-5}	0.22
Ln[1 + (Cw/Ce)]	Flatfishes	8.6×10^{-6}	8.4×10^{-6}	0.02

nonlinear with the reef volume appearing in the numerator and denominator. A comparison reveals that the enhancement model fits slightly better than the aggregation model when the dependent variable is the Ln(1 + CPUEw(t)/CPUEe(t)) and significantly better when the dependent variable is (CPUEw(t) − CPUEe(t))/(CPUEw(t) + CPUEe(t)) ($P < 0.10$; Table 2). Thus, the increase in catch and CPUE in West Shimamaki was not at the expense of East Shimamaki.

The estimate of B (4×10^{-5}) means that 1,000 m^3 of artificial reef increases the catches by 4%. The average biomass contribution of the reef cylinders can be estimated by fitting Equation (1) to the combined East and West catch and CPUE data. This fitted equation estimates that 1 m^3 of artificial reef added an additional biomass to the catches (in kilograms) amounting to the product of 0.018 and fishing effort (in vessel tons). Taking the average level of octopus fishing effort for 1965–1984 as 100 vessel-tons, the increased catch due to the reefs is estimated at 1.8 kg/m^3. Studies of the ecology of *Octopus dofleini* support this finding; the animals are almost always associated with dens, with a single individual per den (Hartwick et al., 1978; Osako and Murata, 1983).

The decline in the values of Ln(1 + CPUEw/CPUEe) relative to the values predicted by the enhancement model in the years 1980, 1983, and 1984 (Fig. 4) may be due to dynamics that are not incorporated in the enhancement model. For example, if the contribution of the artificial reef in increasing the catches is not strictly a linear function of reef volume, especially for a large volume, then the enhancement model will overestimate CPUE in the West in the more recent period when the reef volume was greatest. The same pattern could result from an interaction between fishing effort and the contribution of the artificial reefs. At high levels of fishing pressure (the more recent period), the contribution of the artificial reefs (per unit volume) was less than at lower levels of fishing effort when the standing stock was greater. Several modifications of the enhancement model based on these hypotheses were tested, but their improved fit was not statistically significant, perhaps because of the short CPUE time series. Further, the enhance-

Table 2. Fit of enhancement and aggregation model (E = enhancement; A = aggregation) to octopus catch per unit of effort (CPUE) data

Dependent variable	Model	B	SE	S^2	R^2
Ln[1 + (CPUEw/CPUEe)]	E	4.0×10^{-5}	1.9×10^{-5}	0.036	0.73
Ln[1 + (CPUEw/CPUEe)]	A	7.7×10^{-6}	2.0×10^{-6}	0.050	0.63
$\frac{CPUEw - CPUEe}{CPUEw + CPUEe}$	E	1.6×10^{-4}	3.1×10^{-5}	0.005	0.89
$\frac{CPUEw - CPUEe}{CPUEw + CPUEe}$	A	1.4×10^{-5}	3.2×10^{-6}	0.0147	0.73

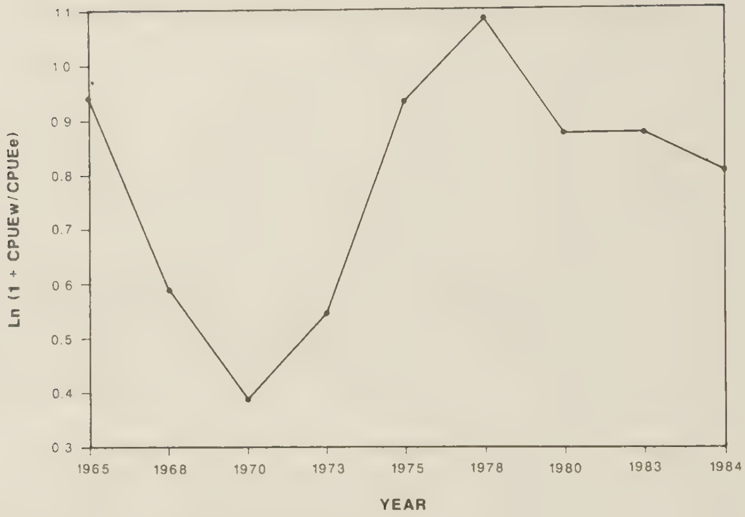


Figure 6. Ln(1 + CPUEw/CPUEe) by year for flatfish.

ment model with only the volume of the small or large reef modules, or with separate parameters for small and large reef modules, did not significantly improve the fit.

FLATFISHES. The catches of flatfishes show considerable annual variation. Although similar in both regions from 1942 to 1959, catches after the beginning of the artificial reef period in 1959 have declined in West Shimamaki and, in the East, have declined, increased, and more recently declined (Fig. 5). Nine vessel censuses in 1965–1984 report the number of gill-net vessels in East and West Shimamaki, and this series is used as the measure of fishing effort for the flatfish resource. The number of gill-net vessels in both regions showed very little change over most of 1965–1984.

The nonlinear regressions of the ratios of catches and CPUE's between West and East Shimamaki fit to the cumulative artificial reef volume (Equations (3) and (4)) for flatfishes give estimates of B that are positive (Table 1, Fig. 6) but not statistically significant ($P > 0.10$). A series of research surveys conducting standardized gill-net fishing at the artificial reef sites in 1977, 1980, and 1981 indicate that flatfishes constitute 30% of the gill-net catches at the artificial reefs (Anonymous, 1985). Thus, the artificial reefs are aggregating the resource but not increasing production for the region. It is possible, however, that the annual variations in catches and CPUE mask the effect of reefs or that the effort measure used was not sufficiently precise.

DISCUSSION

Both flatfishes and octopus are caught at and near the artificial reefs, suggesting that the reefs may be beneficial for these resources. A March 1986 questionnaire completed by 30 and 31 members of the East and West Shimamaki Fishery Associations, respectively, revealed that the reefs are considered beneficial. Generally, the fishermen from the two regions responded similarly to the survey questions. For the two regions combined, 52.5% of the respondents reported using the artificial reefs regularly, 11.5% use them only when fishing elsewhere is poor, and 36% do not use the artificial reefs at all. The gear types most frequently used were gill-net, longline, and octopus fishing gear in the vicinity of the artificial reefs, and pole-and-line gear above the artificial reefs. Flatfishes, scorpionfish (Scorpaenidae), Atka mackerel (*Pleurogrammus monopterygius*), and octopus were commonly caught above and in the vicinity of the reefs. Thirty-three percent of the respondents thought the artificial reefs had expanded the amount of productive habitat, while 38% thought they had not, and 30% could not make a determination.

Unfortunately, the survey did not collect responses for specific resources, but our analysis suggests that the octopus fishermen would be among those who believed the artificial reefs expanded the amount of productive habitat, while the flatfish fishermen would be among those who did not. Our analysis suggests that the octopus are habitat limited, whereas the flatfishes are not but still find the reefs useful perhaps as sites for foraging or orientation.

Although our model expresses catch as a linear function of artificial reef volume and fishing effort, it is likely that this relationship is nonlinear. For example, since increases in fishing effort reduce the standing stock, the need for artificial reefs or the benefits derived from them may vary inversely with the level of fishing effort. Also, the benefits of 1 m^3 of artificial reef volume are likely to be greater if only a few reefs have been deployed than if a large volume of reefs is already in place. The decline below that predicted by our simple linear model of the ratio of the octopus catches in the West to the East since 1978 is possibly due to such nonlinear relationships. Thus the artificial reefs added after 1978 may have contributed less to increased octopus catches in West Shimamaki than the same volume of artificial reefs added when fishing effort, artificial reef volume, or both were lower. Hence, managers need to consider that the benefits of artificial reefs may vary with the level of fishing effort, and regulation of fishing effort should be considered when artificial reefs are deployed.

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8961

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Effect of Seasonal Recruitment on Bias of the Beverton–Holt Length-Based Mortality Estimator

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Abstract.—The Beverton and Holt mortality estimator is a length-based formulation often applied to tropical fish stocks. Although constant uniform recruitment of fish to the exploitable phase is an important condition of its derivation, the robustness of the estimator when this assumption is violated has never been studied. This is important because evidence from the literature shows that in the tropics (i.e., Hawaii) both recruitment and spawning are distinctly seasonal events. Thus, to study properties of the estimator when recruitment is variable, a simple model with seasonal reproduction was developed and analyzed. I show that if age is measured discretely in units equal to the period of the recruitment function, typically 1 year, the age distribution is stationary. The model is extended to length distributions and used as a basis for Monte Carlo simulation of the estimator. Results show that, seasonally, the time of sampling has a major effect on the relative bias of mortality estimates. Bias is negative during periods of increasing recruitment and vice versa, whereas no bias exists at times of maximal and minimal recruitment. Likewise, as the underlying mortality rate increases, bias becomes more severe. When multiple length-frequency samples are drawn and the data and estimates are aggregated, relatively little bias is evident. These results suggest that, when the estimator is used in situations in which recruitment is periodic, it may be better to obtain many small samples than a single large sample, unless some prior information exists concerning the form of the recruitment function.

There has been a resurgence of interest in length-based methods for fishery stock assessment (Jones 1981; Pauly and Morgan 1987). In many situations, these techniques represent an attractive alternative to more conventional stock assessments (Pauly 1982), especially for tropical fishes whose ages are difficult to determine.

In one of the earliest length-based formulations, Beverton and Holt (1956) derived an equation for estimating the total instantaneous mortality (Z) of a fish stock under exploitation. The specific conditions under which their equation is derived are (1) individual fish grow according to a deterministic von Bertalanffy growth curve (i.e., there is no variation among fish within the population in length at age); (2) all fish greater than a minimum length, l_c, are equally vulnerable to the fishing gear and experience a constant total mortality rate (i.e., there are no age- or size-specific differences in mortality); and (3) recruitment to the exploitable stock occurs at a constant uniform rate. When these three conditions are satisfied, mortality can be estimated as

$$Z = K\frac{(L_\infty - \bar{l})}{(\bar{l} - l_c)}; \qquad (1)$$

K and L_∞ are the growth coefficient and asymptotic length, respectively, of the equation, and $\bar{l}$ is the mean length of fish in the catch greater than l_c. Others have investigated and extended this finding (Ssentongo and Larkin 1973; Powell 1979; Wetherall et al. 1987). The estimator has often been used to estimate mortality of fishes in tropical environments (e.g., Munro 1983; Brouard and Grandperrin 1984; Polovina and Ralston 1986), where spawning is more seasonally protracted than in temperate and boreal climates.

In this paper, I investigate the bias of the Beverton–Holt mortality estimator (equation 1) when it is applied under conditions that depart from those for which it was intended. In particular, I relax the assumption of constant uniform recruitment because, contrary to conventional wisdom, most tropical species do not spawn and recruit uniformly throughout the year (Thresher 1984).

Seasonality of Spawning and Recruitment in Hawaii

In a recent summary of spawning and recruitment patterns of Hawaiian fishes, Walsh (1987)

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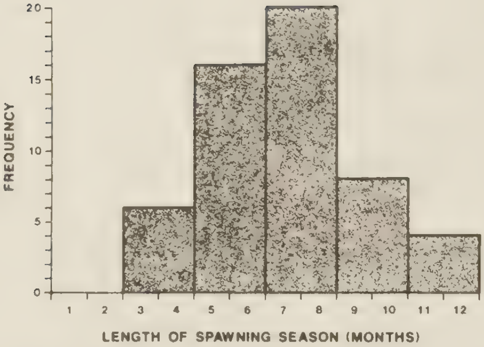

FIGURE 1.—Frequency distribution of the duration of seasonal spawning by fishes in Hawaii (data from Walsh 1987).

tabulated the results of 54 studies involving 48 taxa. In the subtropical Hawaiian environment, spawning lasts for 3–12 months but the average reproductive season is 7 months (Figure 1). Generally, this life history pattern is incompatible with recruitment at a constant uniform rate because larval periods for these fishes typically range from 0.5 to 2.5 months (Brothers et al. 1983; Brothers and Thresher 1985).

This conclusion is further confirmed by the seasonal pattern of recruitment of Hawaiian fishes (Walsh 1987). The frequency with which species recruit within each month varies over the year (Figure 2). For example, two species recruit during January, five during February, and so on. In Hawaii, most species recruit during the spring and summer months, March–August. Overall peak recruitment occurs in June and July. Note that no distinction is drawn between recruitment to reefs and recruitment to offshore exploitable populations, despite the often substantial difference in timing between the two. The greater this difference, the more likely recruitment to the exploitable phase can be approximated by a uniform continuous distribution, even if recruitment to the reef is highly seasonal.

These results demonstrate that reproduction and recruitment of fishes in Hawaii are distinctly seasonal events. Recruitment (R) is cyclic and, as a first approximation, can be reasonably modeled by a simple cosine function (solid line and equation in Figure 2) for which time (t) is measured in years.

Because the constant uniform recruitment assumption is violated, application of equation (1) to length-frequency samples of Hawaiian fishes would constitute a misuse of the method. Nonetheless, the method has been used frequently in tropical and subtropical stock assessments (see above). In such cases, an obvious question arises: To what extent

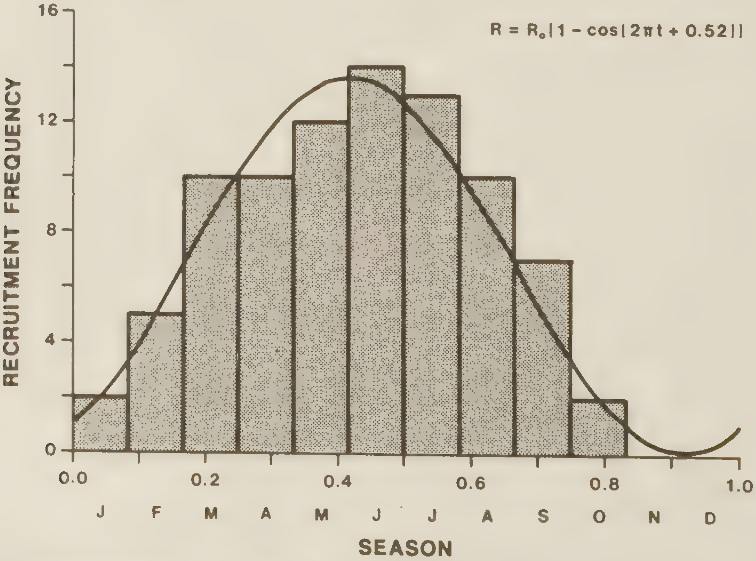

FIGURE 2.—Seasonal frequency of recruitment (R, species per month) for fishes in Hawaii (data from Walsh 1987). The solid line represents the fit of the cosine function to the frequency data; R_0 is a recruitment scaling factor; t is time in years.

does the time of sampling affect mortality estimates? It also is unclear how one should proceed to analyze multiple length-frequency samples taken at different times within the recruitment cycle.

Simple Population Model with Seasonal Recruitment

Here, I alter the hypothetical conditions specified by Beverton and Holt (1956) and develop a model that incorporates a form of seasonal recruitment. To simplify the model, population size is normalized to R_0, the recruitment scaling factor (Figure 2). I therefore define $N(x,t)$ as the relative number of individuals age x alive at time t. Both x and t are continuous variables measured in years. I assume that the population experiences a constant total instantaneous mortality Z, so

$$N(x + 1,t + 1) = N(x,t) \exp(-Z).$$

Moreover, I define the age at the time of recruitment to be 0.0 and specify that the rate of recruitment at time t is

$$N(0,t) = 1 - \cos 2\pi t.$$

The rate is highest midway through the annual cycle, whenever the decimal portion of t equals one-half. Conversely, when t is a whole number at the beginning (or end) of the year, recruitment goes to zero. The population undergoes a standardized seasonal range in recruitment of 0.0–2.0. This natality function lacks the phase-shift parameter (0.52) of Figure 2, also for the sake of simplicity.

When the information specified by the mortality and seasonal recruitment function is combined, it follows that

$$N(x,t) = [1 - \cos 2\pi(t - x)] \exp(-Zx); \quad (2)$$

i.e., the scaled number of individuals of age x alive at time t represents the remaining fish that recruited at time $t - x$ and survived x units of time. Equation (2) provides the basis for examining the effect of seasonal recruitment on mortality estimates. In particular, the relative population size at any time t, $N(t)$, is given by

$$N(t) = \int_0^\infty N(x,t)\, dx$$

$$= \frac{1}{Z} - \frac{Z \cos 2\pi t + 2\pi \sin 2\pi t}{Z^2 + 4\pi^2},$$

so that population size depends only on Z and t. It is easily shown that as Z increases, the maximum in numbers occurs earlier in the annual cycle, and the magnitude of population oscillation increases. Both results are consistent with intuition.

Consider now the age distribution at time t. The population size is $N(t)$, of which $N(x,t)$ are age x. Therefore, the probability density of age x at time t is

$$P_{x,t} = \frac{N(x,t)}{N(t)} = f(x,t,Z).$$

Similarly, the distribution function of age given time is

$$P(X< x_1|t) = \int_0^{x_1} \frac{N(x,t)}{N(t)} dx$$

$$= 1 - \frac{N(t - x_1)}{N(t)} \exp(-Zx_1). \quad (3)$$

This result leads to a remarkable conclusion if fish age is measured in integer values of years, as is commonly practiced. By convention, the true decimal age of fish classified into the integer age-class i is greater than or equal to i, but less than $i + 1$, i.e., increments of age occur on anniversaries of the birth date. Under these conditions, the age distribution is stationary (Figure 3). Note that the ratio $N(t - x_1)/N(t)$ equals 1.0 for all integer x_1. The effect is simply to lag by x_1 discrete cycles. In this special case, the distribution function reduces to

$$P(X < x_1) = 1 - \exp(-Zx_1).$$

Of course, age stationarity depends strongly on identical annual recruitments, certainly the least realistic aspect of the model developed here. For example, the interannual range in recruitment of Hawaiian fishes can be as great as twentyfold (Walsh 1987).

Because the probability distribution for discrete ages is ergodic, it does not matter when a sample is taken in the cycle; all samples will reflect the same age structure. Therefore, in the absence of aging errors, mortality estimates derived from the analysis of age-frequency data (e.g., Chapman and Robson 1960; Robson and Chapman 1961) are unaffected by the cyclical pattern of recruitment modeled here.

Simulated Length Samples

Simulated length data, obtained by transforming ages with an inverted von Bertalanffy growth curve, are now considered. In structuring the simulations, several steps were followed. First, for each length-frequency sample generated, a

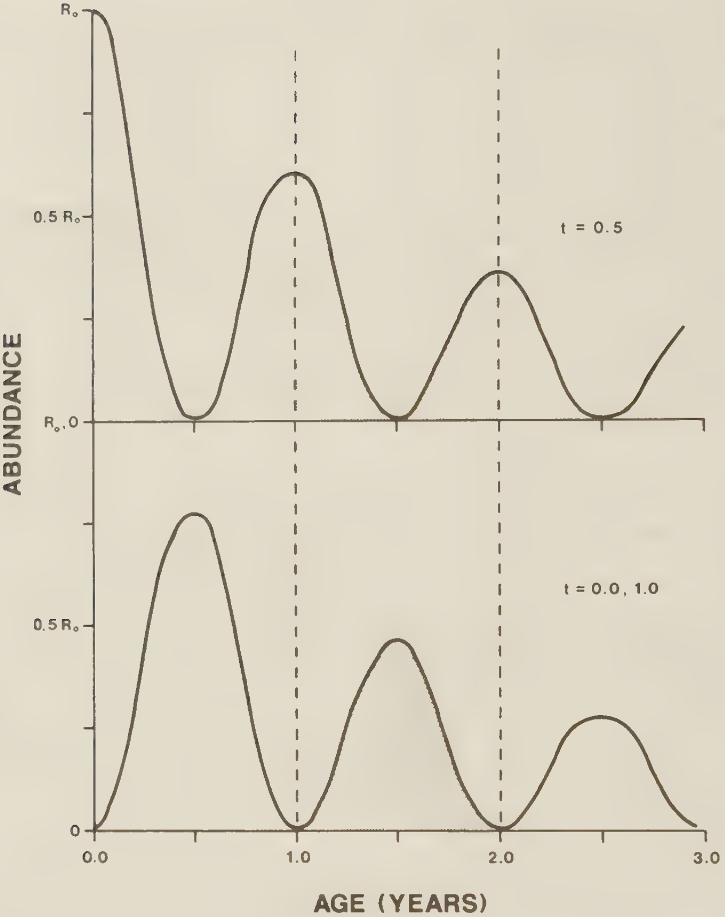

FIGURE 3.—Age-frequency distributions sampled at the beginning (below) and middle (above) of the seasonal recruitment cycle. The numbers of fish of age I are represented by the shaded areas under the curves between 1.0 ≤ age < 2.0. In either case, the proportion of fish of age I is defined by the ratio of the shaded area to the total area under the curve and does not change with time. R_0 is standardized population size; t is time in years.

value of t was randomly selected from a uniform distribution over the range 0.00–1.00 to represent the specific seasonal time of sampling. Next, the age-distribution function formulated in equation (3) was used to define population age structure. Age thus was expressed as a continuous variable. A random age sample of size N was developed by use of the inverse transformation method (Naylor et al. 1966), wherein N uniform random deviates drawn over the range 0.00–1.00 were used to fix values from the age-distribution function of the model population. Numerical solution to the inverse of equation (3) then provided a random age draw from the population. Finally, the randomly selected ages were transformed to lengths by use of a deterministic inverted von Bertalanffy growth equation in which $K = 0.20$ and $t_0 = -0.1$. Depending on the simulation in question (see below). The L_∞ parameter was set to either 20.5 or 50.5. Length-frequency distributions were developed by rounding all lengths to the nearest integer and aggregating the data into length classes. The result was to draw a length sample from the model population illustrated in Figure 4. Single and multiple length-frequency distributions were then analyzed with equation (1) to estimate the underlying mortality rate.

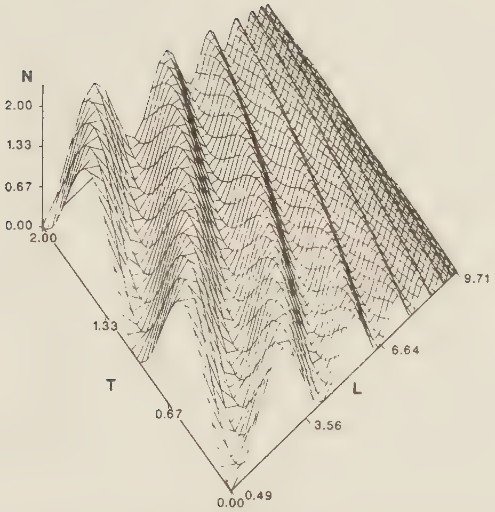

FIGURE 4.—Three-dimensional representation of seasonal (*T*) change in abundance (*N*) of fish at length (*L*).

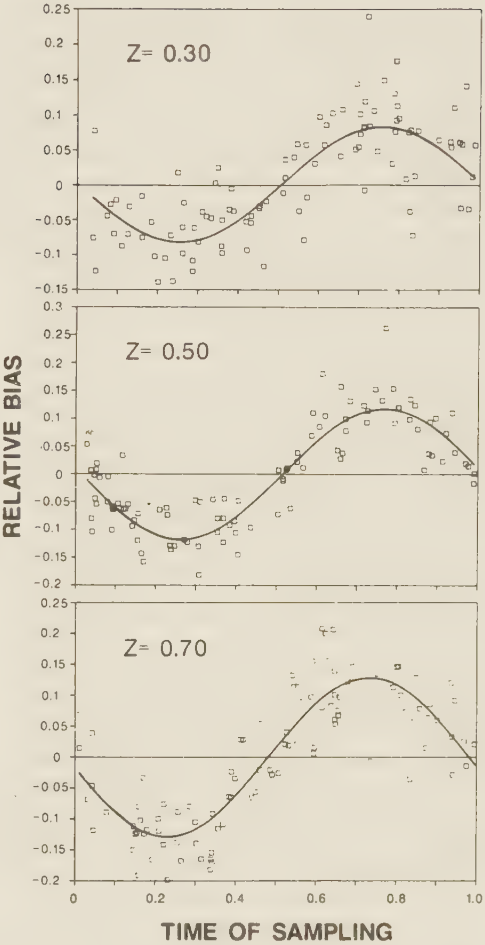

FIGURE 5.—The effect of sampling time and instantaneous mortality (*Z*) on the relative bias of estimates obtained from the analysis of single length-frequency samples. The unit of sampling time is a year.

To examine the effect of sampling time (t) on mortality estimates, Monte Carlo simulations were performed by using 100 samples of size $N = 500$ at each of three different mortality levels ($Z = 0.30$, 0.50, and 0.70 per year). The relative bias, defined as $(\hat{Z} - Z)/Z$, was calculated for each sample estimation and then plotted against t (Figure 5).

The extent of relative bias arising from application of the Beverton–Holt mortality estimator (equation 1) to populations characterized by seasonal recruitment depends on the seasonal time of sampling. In the situation modeled, a negative bias prevailed in estimations completed during the first half of the year, and a positive bias prevailed during the latter half. Roots, at which time no bias exists, occurred at approximately the beginning and middle of the year.

The data were fitted to a sine wave to examine the effect of mortality on relative bias (RB). The model fitted was $\text{RB} = A\sin(2\pi t + \theta)$; A represents amplitude and θ the phase shift. The result (Table 1) is that, as mortality increases, the amplitude of seasonal variation in bias increases. Thus, the greater the underlying mortality, the more serious the consequences of violating the constant uniform recruitment assumption. However, for phase shift, the pattern is not so clear. Over the range $Z = 0.30$–0.70 per year, θ approximated π (3.1416), in which case the roots of the equation equal 0.00 and 0.50. For samples taken at these times, mortality estimates lack bias. Because these times coincide with periods of minimal and maximal recruitment (see the earlier development of the natality function), it may be possible to design a length-frequency sampling program to overcome the bias if the recruitment function is specified.

Monte Carlo simulations also were performed on multiple length-frequency samples to examine the effects of four factors on the propagation of relative bias in the Beverton–Holt mortality estimator. These factors were (a) the total instanta-

TABLE 1.—The effect of mortality on the seasonal expression of relative bias in mortality. The data presented in Figure 5 were fitted to a sine wave model (solid lines in Figure 5) and the amplitude (A) and phase shift (θ) parameters were estimated (standard errors of the estimates are in parentheses). The error mean square (MSE) and reduction in total sums of squares are also provided.

Mortality (Z)	A	θ	MSE	r^2
0.30	0.0814 (0.0068)	3.1062 (0.0962)	0.00260	0.594
0.50	0.1175 (0.0060)	3.0523 (0.0497)	0.00175	0.795
0.70	0.1287 (0.0071)	3.2651 (0.0567)	0.00260	0.769

neous mortality, (b) the number of length categories to which the data are assigned, (c) the manner in which a year's sampling is allocated, and (d) the method of condensing the results.

The effect of mortality on relative bias was examined by simulating the same three levels of Z: 0.3, 0.5, and 0.7. The number of length categories (NCAT) was varied by altering L_∞ (see above) and rounding to the nearest integer. All length data, therefore, were classified into either 20 or 50 categories (assignments to the 0 length interval were rejected). The allocation of sampling effort was studied by varying the number of samples (NSAMP) drawn in a year. Either two samples of size 500 were drawn at randomly selected times t, or five samples of size 200 were taken. In either case, the annual sampling effort was $N = 1{,}000$. Finally, the data were analyzed differently to examine the effect of two methods of condensing the results (COND): averaging or pooling. For the former, each length-frequency distribution obtained was analyzed with equation (1), and the multiple values of $\hat{Z}$ were averaged to estimate the underlying mortality. In the latter, the data from the multiple samplings were pooled before a single analysis was performed. In all cases, the growth parameters K and L_∞ were specified without error (see Majkowski 1982 for discussion).

All four factors were simulated in a balanced design. Because there were three levels of Z, two levels of NCAT, two levels of NSAMP, and two levels of COND, there were 24 treatment combinations. Each then was replicated 50 times, and the relative bias was calculated. Thus, 1,200 annual samplings of size 1,000 were simulated, and the results were analyzed by a fully interactive factorial analysis of variance (ANOVA). Replication of samples 50 times produced an average coefficient of variation for the standard error of the mean equal to 0.76%. This level of precision is sufficient to detect meaningful levels of bias in mortality estimates.

Tables 2 and 3 summarize the findings of the ANOVA with respect to relative bias, the dependent variable. The fully interactive factorial model was significant, but only reduced the total sums of squares by 9.4%. Of the four main effects examined, only Z and NCAT had a significant effect. The treatment mean relative biases for these two factors became more severe as mortality and the number of length classes increased. In both cases, mortality was underestimated, but only slightly.

TABLE 2.—Factorial analysis of variance to examine the effects of mortality (Z), number of length categories (NCAT), number of annual samples (NSAMP), averaging or pooling results (COND), and all interactive terms on the relative bias of the Beverton and Holt (1956) mortality estimator. Asterisks denote $P < 0.05$* or $P < 0.01$**.

Source	df	Mean square	F	Probability of a greater F
Model	23	0.01556	5.28**	0.0001
Error	1,176	0.00295		
Z	2	0.02613	8.86**	0.0002
NCAT	1	0.26380	89.44**	0.0001
COND	1	0.00683	2.31	0.1284
NSAMP	1	0.00223	0.76	0.3846
Z×NCAT	2	0.00817	2.77	0.0632
Z×COND	2	0.00041	0.14	0.8703
Z×NSAMP	2	0.00117	0.40	0.6737
NCAT×COND	1	0.00000	0.00	0.9808
NCAT×NSAMP	1	0.01171	3.97*	0.0465
COND×NSAMP	1	0.00087	0.29	0.5874
Z×NCAT×COND	2	0.00000	0.00	0.9986
Z×NCAT×NSAMP	2	0.00032	0.11	0.8972
Z×COND×NSAMP	2	0.00003	0.01	0.9916
NCAT×COND×NSAMP	1	0.00000	0.00	0.9723
Z×NCAT×COND×NSAMP	2	0.00000	0.00	0.9996

TABLE 3.—Treatment means of the four main effects in the analysis of variance and the single significant interactive term (NCAT×NSAMP).

Factor[a]	Level	Mean relative bias (%)
Z	0.3	−0.83
	0.5	−2.04
	0.7	−2.37
NCAT	20	−0.27
	50	−3.23
COND	Averaged	−1.51
	Pooled	−1.99
NSAMP[b]	2 (500)	−1.88
	5 (200)	−1.61
NCAT×NSAMP	20, 2 (500)	−0.09
	50, 2 (500)	−3.68
	20, 5 (200)	−0.44
	50, 5 (200)	−2.78

[a] Z is mortality, NCAT is number of length categories, COND is method of condensing results, and NSAMP is number of annual samples.

[b] Number of samples (sample size).

For none of the 24 treatment combinations did the mean relative bias exceed 5.2%. Due to the large number of F tests in Table 2, the single significance ($P = 0.05$) of an interaction term (NCAT*NSAMP) probably was due to a type-I error. In the absence of real differences the probability of such an error in 15 tests is 0.54; in 13 tests, it is 0.49.

Discussion

The results presented here show that the integer-age probability distribution, developed under a model of seasonal recruitment (Figure 2), is stationary. Although the cosine natality equation represents only one of many potential recruitment functions, the conclusion is more general. As long as (a) recruitment is qualitatively and quantitatively the same from year to year and (b) age is measured discretely in some multiple of the recruitment period, the population age structure will remain stationary in spite of reproductive seasonality (see Figure 3; Keyfitz 1968).

As suggested by Munro (1982), the seasonal time of sampling has a major influence on the relative bias of mortality estimates calculated from samples taken at only one time of the year (Figure 5). This effect is due to seasonal variation in the mean size ($\bar{l}$) of individuals in the population (Ebert 1973). The problem may be overcome by sampling at times when recruitment is either maximal or minimal, but to do so requires additional information to specify the recruitment function. Furthermore, the generality of this sampling strategy is open to some question and needs more work.

Still, the average of several mortality estimates obtained by sampling at random times within the year showed little bias. Under these conditions, Monte Carlo simulations demonstrated that the Beverton–Holt (1956) mortality estimator is fairly insensitive to violation of the constant uniform recruitment assumption. Over a broad range of simulated conditions, the maximum relative bias observed was −5.2% of the underlying parameter, and the average relative bias was only −2.1%. Practically speaking, these biases are negligible. The simulations also showed that mortality estimates from several seasonally distinct length-frequency distributions were equivalent, whether individual estimates were averaged or the data were pooled. Similarly, no bias effect was evident when the sampling structure was altered to represent a few large samples or many small ones.

These findings indicate that, if equation (1) is used to estimate the mortality of a population that experiences substantial seasonal variation in recruitment, many small length samples pooled together may be preferable to a single large sample. Pooling of data obtained from throughout the year results in an integrated representation of the average size structure. Moreover, when a field sampling program is planned, advance knowledge of the recruitment function provides the investigator with information useful in determining the optimum times for sampling.

Although the results presented here show that the Beverton–Holt mortality estimator is robust with respect to seasonal recruitment, other difficulties may well arise, due either to sampling error or to violation of one or more of the remaining assumptions. For example, Majkowski (1982) performed a sensitivity analysis to study the effects of misspecifying the four parameters of equation (1). Perturbation of the L_∞ parameter by some percentage δ, for example, alters Z by roughly 2δ. The formula is even more sensitive to changes in $\bar{l}$ and l_c. Similarly, violations of other assumptions of the model (i.e., constant total mortality rate, constant selectivity, and deterministic von Bertalanffy growth) likely would bias estimates of Z. Because the robustness of the estimator to these types of departures has yet to be examined, caution is recommended with the estimator's use.

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8962

NUMERICAL INTEGRATION OF DAILY GROWTH INCREMENTS: AN EFFICIENT MEANS OF AGEING TROPICAL FISHES FOR STOCK ASSESSMENT

Stephen Ralston[1] and Happy A. Williams[2]

ABSTRACT

For an objective, cost-effective ageing methodology applicable to tropical species, a new approach to estimating parameters of the von Bertalanffy growth equation through the study of otolith microstructure was developed and applied to *Pristipomoides zonatus*, a deepwater snapper widely distributed throughout the Indo-Pacific region. The average width of sagittal daily growth increments was used to measure otolith growth rate, which was then related to the size of the otolith. The data were numerically integrated, providing estimates of age (in years) at regular 500 μm increments to otolith length, which was then used to predict fork length (FL mm) at age with regression analysis. The data were fitted to the von Bertalanffy growth model, resulting in $FL = 442 (1 - \exp(-0.234 (Age + 0.892)))$.

The method was critically examined and validated through the study of 1) annual hyaline and opaque markings that appear in the otoliths, 2) Monte Carlo simulation, 3) length-frequency analysis, 4) examination of spawning seasonality relative to back-calculated birth date taken from the time of first annulus formation, and 5) empirical comparisons with the literature concerning snapper growth.

Developing stock-assessment models tailored to the characteristics and needs of tropical fisheries is an area of active and productive research. In particular, significant progress has been made over the last several years in the area of length-based methods (Schnute and Fournier 1980; Jones 1981; Pauly 1982, 1987b; Fournier and Breen 1983; Fournier and Doonan 1987; Schnute 1987). With these advances, a powerful array of biologically realistic models is now available for analyzing length-frequency data.

Although tremendous strides have been made in developing these new length-based methods, the importance of acquiring other information besides length-frequency data and total catch statistics is all the more evident. Ancillary information usually helps to stabilize and improve the estimation of model parameters (Schnute and Fournier 1980; Fournier and Doonan 1987). Foremost is developing an independent knowledge of growth dynamics (Gulland 1987; Morgan 1987). It is now generally accepted that the analysis of length-frequency data, in conjunction with age estimates derived from the study of hard parts, represents the most promising avenue for future assessment work on exploited tropical species (Pauly 1987a).

Nonetheless, estimating growth rates of tropical species by using otoliths has been a difficult and persistent problem. Investigators have often failed in their efforts, either because of an absence of conventional hyaline and opaque markings, as is true of most tropical species, or because of an aversion to direct enumeration of daily otolith increments. The latter can be an extremely difficult, time consuming, and tedious process.

Since Pannella (1971) first discovered the existence of daily otolith increments, a large body of work has developed on the subject. While many investigators have touted the potential benefits of ageing tropical species by using otolith microstructure, few have attempted to develop growth curves with assessment goals specifically in mind. Instead, most work to date has dealt with ageing larval forms (Jones 1986) and elucidating endogenous and environmental effects on increment formation (Campana and Neilson 1985). Although much useful information has been gained, daily increments have yet to fulfill their promise with respect to applications in the area of juvenile and adult population dynamics.

The purpose of this study was to develop a general method of ageing tropical fishes by using daily

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growth increments, specifically with stock-assessment applications in mind. In this regard, the von Bertalanffy growth equation (Ricker 1979) is of fundamental importance. Due to its widespread use in assessment models (e.g., the Beverton and Holt [1957] yield formulation), parameter estimates for this equation provide an ideal complement to many of the length-based methods that are currently in use (e.g., Morgan 1987). The ultimate goal of this study was, therefore, to develop a methodology to estimate the von Bertalanffy growth parameters K and L_∞ from the study of daily increments. Ideally, the approach developed should be general in its application, easy to implement, simple in its technical requirements, and cost effective. Were such a uniform framework to the study of age and growth of exploited tropical species developed, it would assist routine assessment work greatly.

MATERIALS AND METHODS

As part of a larger program to assess stocks of deep slope fishes in the Mariana Archipelago (Polovina 1985; Polovina and Ralston 1986; Ralston in press b), a study of the age and growth of gindai, *Pristipomoides zonatus*, was initiated. This commercially important eteline snapper (Lutjanidae) is widely distributed in the Indo-Pacific region (Allen 1985) and is the most commonly caught species in Guam's deepwater hook-and-line fishery (Polovina 1986).

Field sampling for gindai specimens was conducted from the NOAA ship *Townsend Cromwell* during the 2 yr period spanning April 1982 to May 1984. During this time, six 40 d cruises were completed, such that samples of gindai were obtained during all months of the year except March, September, and October.

All gindai were caught during daylight hours by using hydraulic fishing reels equipped with circle fish hooks. When landed, fish were measured to the nearest millimeter fork length (FL) with a measuring board and weighed to the nearest 0.01 kg on a beam balance.

Specimens were sexed at the time of capture by gross examination of the gonads. In addition, a representative selection of the gonads was frozen for more detailed examination in the laboratory. There, they were preserved in a solution of 10% buffered formalin and weighed to the nearest 0.1 mg. Ovaries were staged with the classification of Everson (1984), developed for *Etelis carbunculus*, a related deepwater eteline lutjanid. His classification recognizes seven stages based on egg size, shape, and yolk content, i.e., (I) primordial, (II) early developing, (III) developing, (IV) advanced developing, (V) early ripe, (VI) ripe, and (VII) residual. Gonadosomatic indexes (gonad weight expressed as a percentage of body weight) also were calculated where possible.

Otoliths

At the time of capture, sagittal otoliths were collected, by frontal section through the cranium, from certain individuals sampled uniformly from the full size range of gindai captured. The otoliths were rinsed in fresh water to remove adhering membranes and endolymph and were stored dry in glass vials. Later in the laboratory, they were examined with a dissecting microscope for the presence of hyaline (i.e., translucent) and opaque markings while illuminated with reflected light against a dark background. When markings were present, the distance from the focus to the beginning of each opaque zone was measured along the postrostral growth axis by using a calibrated ocular micrometer. Total otolith length (focus to postrostrum) also was recorded.

A random subsample of gindai otoliths was taken, and their microstructure examined for the presence of daily increments (Campana and Neilson 1985). To prepare the otoliths, they were first embedded in casting resin, which was allowed to harden completely. Cast otoliths were sectioned on a Buehler[2] ISOMET low speed jewelry saw. Thin (0.70 mm) sections were made through the focus along a frontal plane to the most distal portion of the postrostrum. Sections were polished sequentially on a Buehler ECOMET polisher/grinder with 180 and 600 grit abrasive disks. Samples were then briefly etched for 5–30 seconds in a dilute solution of 1% HCl, washed in water, and dried. Prepared sections were mounted on glass slides with Euparol or Flotexx and cover slips and allowed to clear and harden completely prior to viewing (approximately 2 weeks).

Mounted otolith sections were examined with a compound binocular microscope by using transmitted light at a magnification of 200 or 400×. Total lengths of the otoliths (i.e., the distance in micrometers between the focus and the postrostral margin) were measured ($N = 94$) and individual readings were made at selected points along the postrostral growth axis, wherever it was possible to distinguish the characteristic bipartite structure of daily increments. At each site sampled the average width of presumptive daily growth increments was determined by counting a small number (me-

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

dian = 14, range = 5–22) of increments and measuring the axial length of the short segment in which they occurred. In addition, the curvilinear distance between the midpoint of each segment and the otolith focus was measured along the focus to postrostral growth axis. Up to 12 readings were made from each preparation. The focus was defined to be the most posterior of what typically were several primordia (e.g., Radtke 1987).

The data were summarized by computing the ratio of segment length in micrometers to the included number of increments at each specific site examined, providing an estimate of the average increment width at some measured distance from the otolith focus. Under the assumption that one increment forms each day, these data can be used to estimate the instantaneous growth rate of the otolith (Ralston and Miyamoto 1981, 1983; Ralston 1985).

To estimate age, a simple form of numerical integration was employed. Starting at the focus, the data were subdivided into 500 μm intervals of otolith length. For each interval, the arithmetic mean growth rate of the otolith was calculated based upon the number of readings falling therein. This average growth rate was then divided into 500 μm to estimate the number of days needed to complete growth through the intervals, which were sequentially accumulated away from the focus, and finally divided by 365.25 to convert age estimates to years. The size of the otolith upon completion of growth through each interval was used to predict the corresponding FL of the fish after the natural logarithm of FL was regressed on the logarithm of total otolith length. These data (age [in years] and FL [mm]) were then fitted to the von Bertalanffy growth equation (Ricker 1979) by using a nonlinear regression routine (SAS Institute Inc. 1979, NLIN procedure).

Monte Carlo simulation techniques (Naylor et al. 1966) were applied to this analytical procedure to evaluate the accuracy (i.e., bias) of the estimator and to study the precision of parameter estimates. The structure of the simulation model was such that von Bertalanffy growth was assumed by stipulating a decreasing linear relationship between somatic growth rate and length, i.e., $d(\mathrm{FL})/dt = K(L_\infty - \mathrm{FL})$. Likewise, the relationship between otolith length (OL) and FL was assumed to be governed by the power function, so that $\mathrm{FL} = \alpha \mathrm{OL}^{\beta}$. Otolith growth rate, $d(\mathrm{OL})/dt$, was then obtained by forming the ratio of $d(\mathrm{FL})/dt$ and $d(\mathrm{FL})/d(\mathrm{OL})$. All parameters in the model were otherwise set equal to the estimates obtained from the otolith study, and the specific probability distributions invoked were similar to those encountered with the actual data.

Length-Frequency Analysis

As an independent means of verifying results obtained through the study of otoliths, the regression method of Wetherall et al. (1987) was used to estimate specific growth and mortality parameters characterizing the study population. The analysis was based on the combined length-frequency distribution (FL rounded to the nearest 10 mm) of all gindai sampled (see Ralston [in press a] for a discussion of the effects of pooling length data taken at different times throughout the year).

Initially, this method requires determination of the least FL at which fish are fully represented in the catch ($\ell^{*}_{c,\min}$). For this purpose, the first size class larger than the mode was assumed to be the smallest length category fully sampled (see, for example, Ricker 1975). Moreover, for this and any larger cutoff value ($\ell_{c,i}$), we were able to compute the mean size of fully vulnerable fish in the catch ($\bar{\ell}_i$), i.e., those fish greater than $\ell_{c,i}$. As $\ell_{c,i}$ was successively advanced through the fully vulnerable size range, the mean and variance in size of larger fish were recalculated at each step, and a series of ordered pairs was developed. The actual estimation procedure involved regressing values of $\bar{\ell}_i$ against successive values of $\ell_{c,i}$. The inverse of the standard error of $\bar{\ell}_i$ was used as a statistical weight for each point, leading to the best linear unbiased estimates of the slope (δ) and intercept (ζ). With the resulting regression statistics, the formulae provided in Wetherall et al. (1987) were used to obtain point estimates of the ratio of total instantaneous mortality rate to the von Bertalanffy growth coefficient (Z/K) and the von Bertalanffy asymptotic size parameter (L_∞). In particular, they showed that $Z/K = \delta/(1 - \delta)$ and $L_\infty = \zeta/(1 - \delta)$. Likewise, error estimates for these statistics were calcuated as well.

RESULTS

Age Estimation from Increment Microstructure

In all, 440 otoliths were extracted, and of these, 94 were sectioned and examined for daily increments. As expected, there is a clear statistical basis for predicting FL from OL (Fig. 1). The regression equation relating these variables is highly significant ($P < 0.0001$) and is given by

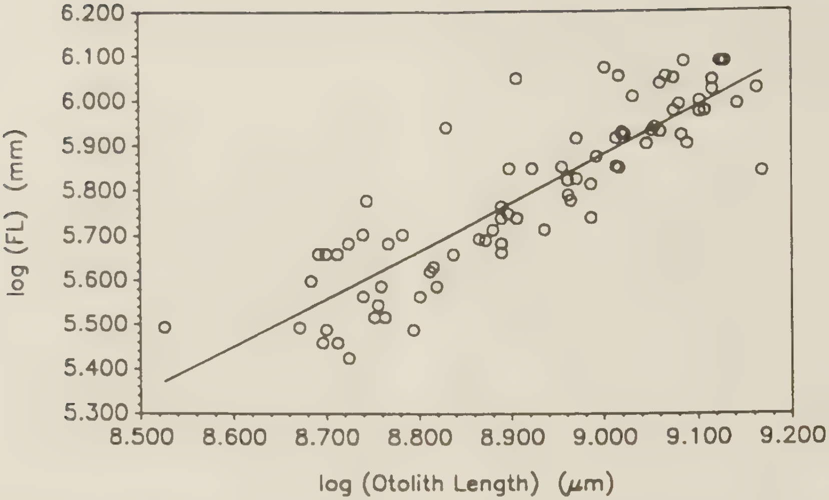

FIGURE 1.—Regression of the natural logarithm of FL on the log of otolith length (OL) (focus to distal margin of postrostrum).

$$\log(FL) = -3.783 + 1.074 \log(OL),$$

with $r^2 = 0.76$ and standard errors for the slope and intercept equal to 0.0634 and 0.5665, respectively.

The sagittae of gindai display microstructure (Fig. 2) typical of daily increments observed in other studies (Dunkelberger et al. 1980; Tanaka et al. 1981; Watabe et al. 1982). Light incremental zones and dark discontinuous zones are clearly visible in the photomicrograph. One daily growth increment is composed of the bipartite combination of a single

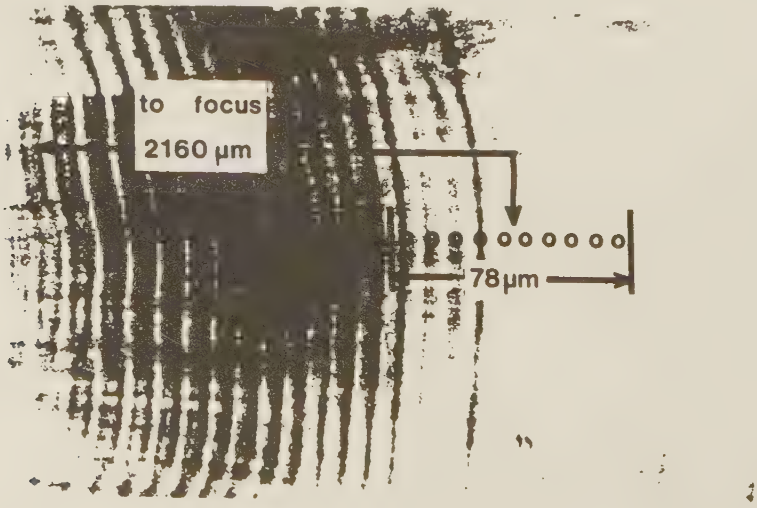

FIGURE 2.—Photomicrograph of a sectioned gindai otolith showing increment microstructure. The 10 daily increments in a short 78 μm segment are enumerated and increment width, i.e., otolith growth rate, is calculated (7.80 μm/d). The distance to the focus is also shown (2,160 μm).

incremental zone with its adjacent discontinuous zone. When counting daily increments, we enumerated the dark discontinuous zones.

From the 94 sectioned otoliths examined for the presence of growth increments (Fig. 2), a total of 852 determinations of otolith growth rate (i.e., increment width) were completed. Note that no increment width data were collected at otolith lengths in excess of 7,500 μm, although otoliths as long as 9,594 μm were measured and used in the regression analysis of log(FL) on log(OL) (see Figure 1). Beyond 7,500 μm (corresponding to 329 mm FL), the pattern of otolith growth became increasingly irregular, and clearly distinguishable daily increments, composed of well-defined incremental and discontinuous zones, were difficult to resolve.

The data show that as otolith length increased the growth rate of the otolith declined (Fig. 3). No detectable difference in the relationship between otolith growth rate and otolith length could be attributed to sex. A partitioned analysis of covariance of the log-transformed data (Table 1) failed to reveal differences in either the slopes or adjusted means of males and females. Thus, data for the two sexes were combined.

The mean growth rate of the otolith $d(\mathrm{OL})/dt$,

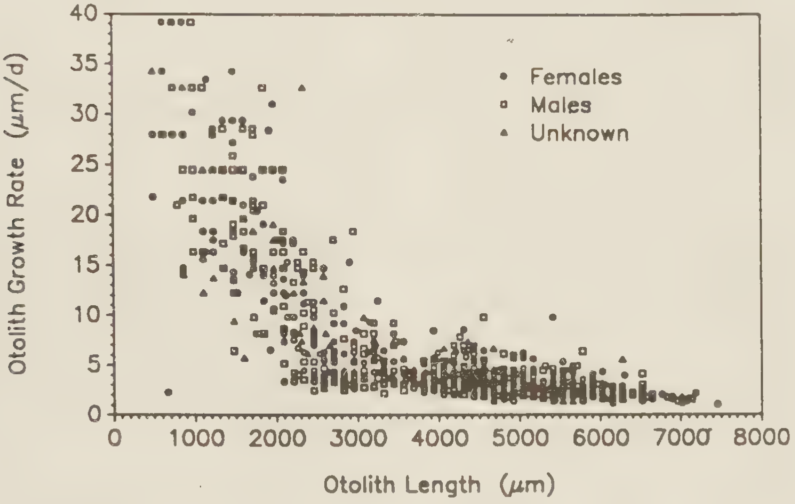

FIGURE 3.—The relationship between otolith growth rate and otolith length plotted for males, females, and specimens of unknown sex.

TABLE 1.—Partioned analysis of covariance of log-transformed otolith growth rate $d(\mathrm{OL})/dt$. Otolith length (OL) was used as the covariate and sex was the treatment variable. The data were divided into two separate linear partitions: data for which OL ≤3,700 μm and OL >3,700 μm.

Source	df	Sum of squares	Mean square	*F*	*P*
OL ≤3,700 μm					
Equality adjusted means	1	0.0015	0.0015	0.01	0.935
Zero slope	1	121.9917	121.9917	551.78	0.001
Error	316	69.8635	0.2219		
Equality slopes	1	0.7158	0.7158	3.26	0.072
Error	315	69.1477	0.2195		
OL >3,700 μm					
Equality adjusted means	1	0.1334	0.1334	1.14	0.286
Zero slope	1	15.9656	15.9656	136.72	0.001
Error	389	45.4273	0.1168		
Equality slopes	1	0.2202	0.2202	1.89	0.170
Error	388	45.2071	0.1165		

and the variance in growth rate σ^2_i within each of the $i = 1,15$ intervals of otolith length (Table 2) show that as otolith length increased both $d(\mathrm{OL})/dt$ and σ^2 declined. The estimated age (in years) at the point of transition between each of the 15 otolith length intervals (i.e., upon completion of growth through interval k) was

$$\mathrm{Age}_k = \frac{1}{365} \sum_{i=1}^{k} \frac{\Delta(\mathrm{OL})}{d(\mathrm{OL})/dt_i},$$

where $\Delta(\mathrm{OL})$ is 500 μm in the application presented here.

Otolith length upon completion of growth through interval k was converted to the equivalent FL (see Figure 1), and the data fitted to the von Bertalanffy growth equation. Because this model poorly represents growth during the early life history, only data representing otolith length intervals in excess of 3,000 μm (i.e., ages >0.8 year) were used in the regression analysis (see Discussion). Table 2 also provides a statistical weight for each of the age estimates. Weighting was desirable because 1) the sample size of each mean varied, 2) the σ^2_i were heterogeneous (proportional to the square of the mean), and 3) compounding of error occurred because of the additive property of the estimator. Weights were calculated as the reciprocal of the sum of standard errors of the means through interval k. The weighted least squares fit to the von Bertalanffy equation (Fig. 4) was

$$\mathrm{FL} = 442\ (1 - \exp(-0.234\ (\mathrm{Age} + 0.892))),$$

with 99.99% of the total variation in FL explained by the model, and with asymptotic standard errors for L_∞, K, and t_0 equal to 14.85 mm, 0.0180 yr^{-1}, and 0.078 year, respectively.

The results of the Monte Carlo simulation indicate that the estimation procedure was unbiased. Following 50 computer replications of the same sampling procedures outlined above, there was no detectable bias in the estimation of either K or L_∞, even though the coefficients of variation for the standard errors of these statistics were both small (0.64 and 0.34%, respectively). Moreover, variance estimates derived from the approximately normal simulation sampling distributions of K and L_∞ provided a basis for placing confidence intervals on the point estimates as follows: $P(0.213 < K < 0.255) = 0.95$ and $P(421 < L_\infty < 463) = 0.95$.

Annual Marks on the Otoliths

On occasion, hyaline and opaque zones were evident in the sagittae of gindai (Fig. 5). These were most easily viewed with light reflected off otoliths immersed lateral side up in water. Typically, however, the zonations were poorly developed or absent entirely. Nonetheless, of the 440 otoliths examined, some banding was evident in 171 (39%), and it was possible to classify the margins of these as either hyaline or opaque. The seasonal expression of hyaline or opaque zones on the margins of these otoliths shows what appears to be an annual periodicity; otoliths sampled during the November–December bimonthly period were characterized almost exclusively by the presence of hyaline margins (94%). Just 2 months later (January–February), only 13% of the otolith samples were similarly classified (Fig. 6). Thereafter, the percentage of otoliths with hyaline margins was never elevated, at least through the

TABLE 2.—Summary statistics of otolith growth by 500 μm intervals in otolith length.

Otolith length interval	Lower bound	Upper bound	N	Mean growth rate (μm/d)	Variance growth rate	Interval duration (d)	Age (yr)	Statistical weight
1	1	500	3	28.03	39.20	17.84	0.0	0.0696
2	501	1,000	30	27.89	90.28	17.93	0.1	0.0164
3	1,001	1,500	55	21.53	42.81	23.22	0.2	0.0132
4	1,501	2,000	60	18.43	41.68	27.14	0.2	0.0118
5	2,001	2,500	83	10.94	32.57	45.70	0.4	0.0115
6	2,501	3,000	71	5.97	12.76	83.68	0.6	0.0115
7	3,001	3,500	54	5.52	4.41	90.55	0.8	0.0114
8	3,501	4,000	49	3.99	1.61	125.25	1.2	0.0113
9	4,001	4,500	110	3.98	2.18	125.54	1.5	0.0113
10	4,501	5,000	99	3.36	1.72	149.02	1.9	0.0113
11	5,001	5,500	95	3.01	1.55	165.98	2.4	0.0112
12	5,501	6,000	78	2.87	1.03	174.03	2.9	0.0112
13	6,001	6,500	39	2.29	0.74	217.91	3.5	0.0112
14	6,501	7,000	18	2.03	0.45	246.60	4.1	0.0112
15	7,001	7,500	7	1.51	0.16	330.97	5.0	0.0111

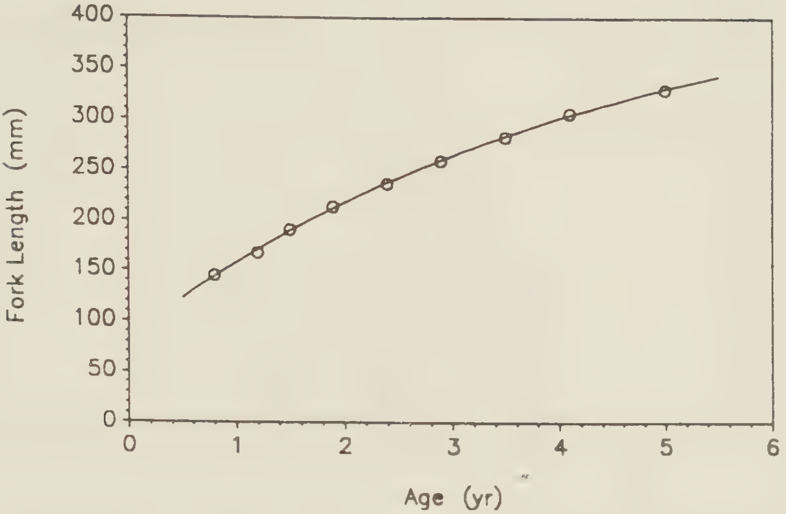

FIGURE 4.—Von Bertalanffy growth curve for gindai developed from the study of daily growth increments.

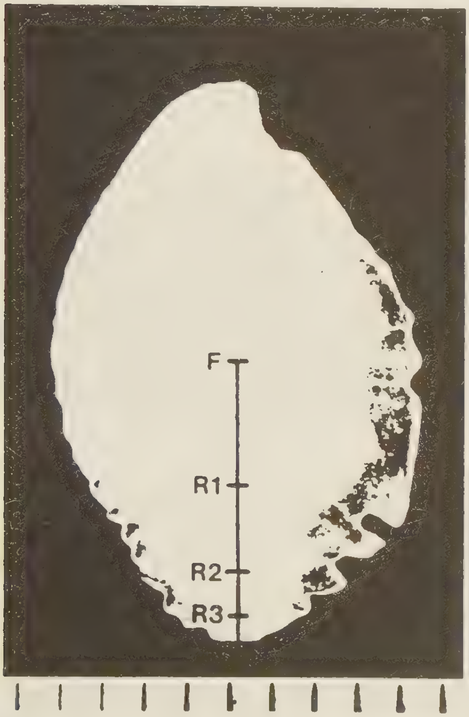

FIGURE 5.—Photomicrograph of a whole gindai sagitta showing the development of hyaline and opaque zones and distance measurements from the focus (F) to the otolith margin and each ring group.

end of August. No data were available for the months of September and October. These results indicate that the markings observed were annular and that the opaque zone first began to form during January–February.

Given the apparent annual periodicity of the markings, growth was estimated by examining their spatial pattern within the otolith. Table 3 presents mean otolith radii measured to the start of each new opaque zone, summarized by sampled age groups, for the 29 specimens that showed well-developed markings throughout their sagittae (e.g., Fig. 5). The table also presents the weighted mean radii converted to estimated FL's by using the regression developed earlier (Fig. 1).

The assembled data were then used to estimate

TABLE 3.—Back-calculated lengths based on annual markings in gindai otoliths. All measurements were taken along the focus to postrostrum growth axis.

		Mean otolith radius (μm) at annulus				
Age group	*N*	I	II	III	IV	V
I	0	—				
II	0	—	—			
III	6	3,233	4,700	5,600		
IV	13	3,054	4,400	5,408	6,315	
V	10	3,130	4,440	5,610	6,530	7,260
Weighted mean (μm)		3,117	4,476	5,517	6,409	7,260
Standard deviation		222	349	427	468	443
Fork length (mm)		128	189	237	278	318

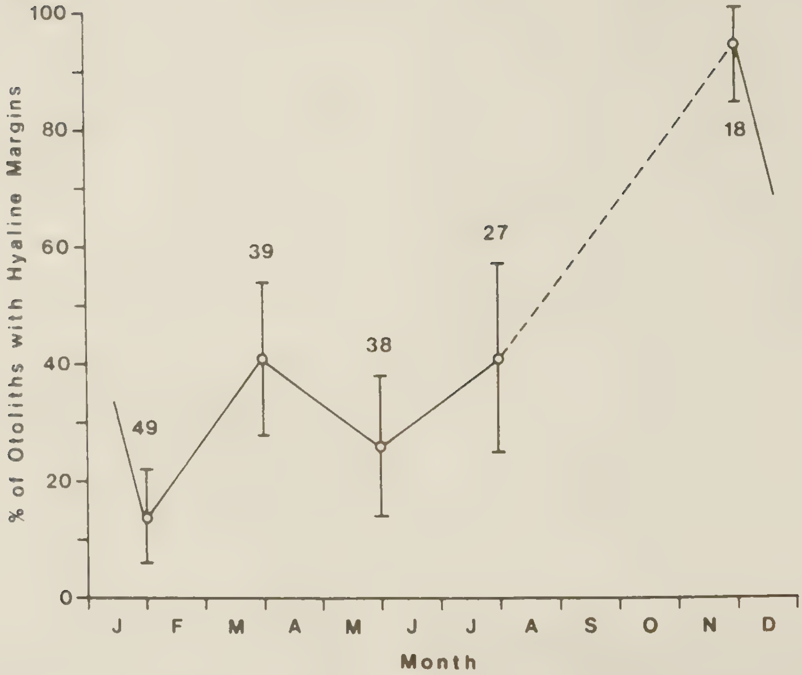

FIGURE 6.—The seasonal occurrence of hyaline and opaque markings on the margins of gindai otoliths.

parameters of the von Bertalanffy growth equation by means of a Walford plot (Ricker 1975), wherein results from a regression of FL at time $t + 1$ against FL at time t provide the basis for estimates of $K = 0.156$ yr^{-1} and $L_\infty = 537$ mm FL.

Length-Frequency Analysis

The combined length-frequency distribution for all gindai sampled (Fig. 7) shows that the mean size was 368 mm FL (standard deviation = 43.1 mm). Fish ranged in size from 190 to 490 mm FL and the modal size was 380 mm FL. Thus, $\ell_{c,\min}$ was estimated to be 385 mm FL. There is evidence to show that, above this size, fish were equally vulnerable to the gear (Ralston 1982, unpubl. data), although smaller individuals were almost certainly underrepresented in the catch because of the selective sampling action of the fish hooks. As $\ell_{c,i}$ increased from 385 to 485 mm FL, the corresponding value of $\bar{\ell}_i$ increased (Table 4). Due to a sample size of one, estimates of the variance and standard error of the mean could not be calculated when $\ell_{c,i} = 485$ mm. Without a statistical weight, the point was excluded from the analysis.

The regression of $\bar{\ell}_i$ on $\ell_{c,i}$ (Fig. 8) was highly significant ($P << 0.0001$), although there was an increasing lack of fit as $\ell_{c,i}$ increased, especially beyond 435 mm FL. This result was due to the diminished statistical weights accorded these points (Table 4). Estimates of the slope and intercept of the regression were $\delta = 0.7051$ and $\zeta = 137.31$, with standard errors of 0.0200 and 8.138, respectively. Thus, the mortality to growth ratio (Z/K) is esti-

TABLE 4.—Length-frequency data fitted to the Wetherall et al. (1987) regression model for estimating Z/K and L_∞ (fork length in mm).

Class fork length	N	$\ell_{c,i}$	$\bar{\ell}_i$	Variance	Standard error	Relative statistical weight
390	362	385	409.5	284.4	0.438	22.82
400	314	395	415.9	212.1	0.435	22.94
410	301	405	422.1	157.3	0.441	22.65
420	214	415	429.3	110.7	0.469	21.32
430	165	425	436.3	79.4	0.523	19.10
440	83	435	444.6	62.1	0.705	14.18
450	30	445	453.8	58.3	1.178	8.49
460	10	455	463.3	78.7	2.562	3.90
470	1	465	480.0	200.0	10.000	1.00
490	1	485	490.0	—	—	—

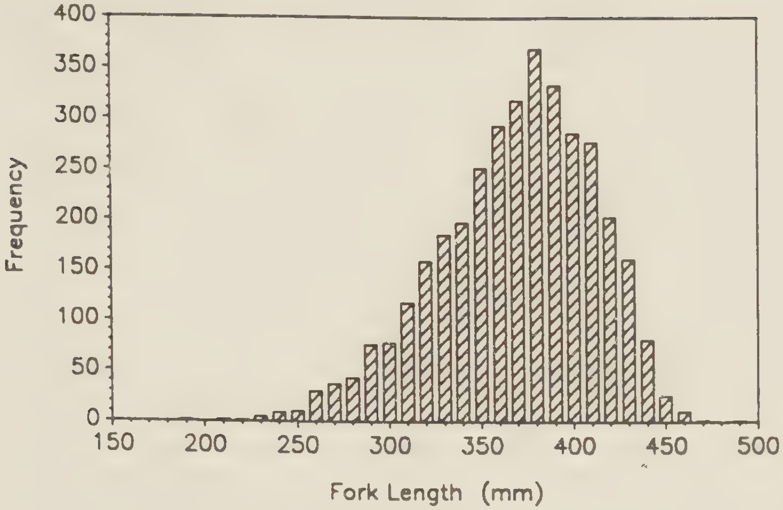

FIGURE 7.—Combined length-frequency distribution for all gindai sampled.

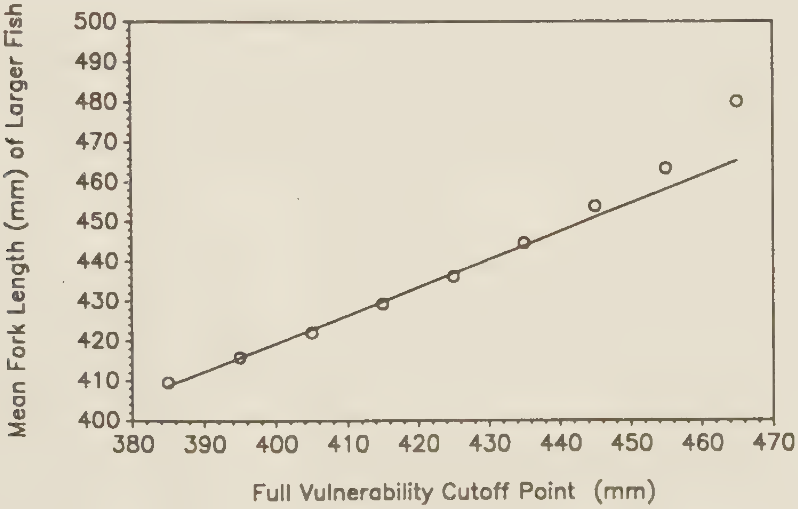

FIGURE 8.—Wetherall et al. (1987) regression of $\bar{\ell}_i$ on $\ell_{c,i}$ (see text for further discussion).

mated to be 2.39 and L_∞ = 466 mm FL. Confidence intervals for these estimates are $P(1.94 < Z/K < 2.62) = 0.95$ and $P(458 < L_\infty < 474) = 0.95$.

With the results presented earlier, it is possible to decompose the Z/K ratio and estimate total mortality rate (Z). For $K = 0.234$ yr^{-1} (increment microstructure), $Z = 0.56$ yr^{-1}, and for $K = 0.156$ yr^{-1} (annual marks), $Z = 0.37$ yr^{-1}.

Spawning Season

Gonadosomatic indexes for male and female gindai are summarized by month of capture in Figure 9. The relative size of gindai ovaries was considerably greater than the testes. More importantly, there was a distinct seasonal trend in the monthly mean gonadosomatic indexes of females, which

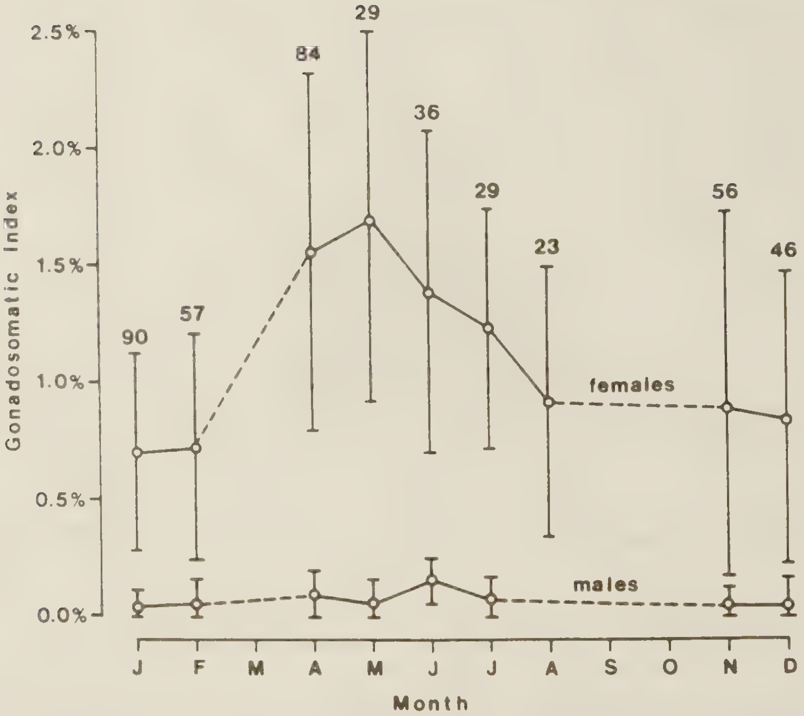

FIGURE 9.—The seasonal pattern of variation in mean gonadosomatic indexes of male and female gindai in the Mariana Archipelago. Note that mean index values are bracketed by sample standard deviations with the sample sizes given above.

reached a peak in May and diminished as the summer progressed.

The same pattern was mirrored in the percentage of ovaries classified to stages IV–VI (i.e., advanced developing to ripe). During the January–March quarter, only 1.4% of the ovaries sampled were so classified. This statistic rose to 48.3% during the April–June period, but then dropped to 19.2% in the July–September quarter and to 16.7% over the last quarter of the year (October–December). The similarity of these two patterns reinforces the interpretation of reproductive seasonality based on gonadosomatic indexes alone (but see deVlaming et al. 1982), and when taken together, these data indicate that peak spawning of gindai in the Mariana Archipelago occurs in late May and early June.

DISCUSSION

Other researchers also have measured the width of daily increments to study fish growth. Methot (1981) used the widths of the outermost three increments in the otoliths of *Engraulis mordax* and *Stenobrachius leucopsarus* as a measure of recent somatic growth rate. Brothers and McFarland (1981) measured the thickness of daily increments in newly recruited *Haemulon flavolineatum* to discriminate life history transitions, as did Gutiérrez and Morales-Nin (1986) in their study of *Dicentrarchus labrax*. Moreover, integration of increment width data to estimate age has been reported, both analytically for *Pristipomoides filamentosus* (Ralston and Miyamoto 1981, 1983) and numerically for *Merluccius angustimanus*, *Merluccius* sp., *Engraulis mordax*, and *Pristipomoides auricilla* (Brothers et al. 1976; Methot 1983; Ralston 1985).

Experimental work has revealed some of the factors that affect the width of daily growth increments. For example, decreased somatic growth in *Oncorhynchus tshawytscha* due to reduced temperature also results in reduced increment thickness (Neilson and Geen 1985). There is conflicting evidence, however, regarding the effect of food ration on daily increment width. Volk et al. (1984) experimentally altered somatic growth rates of *O. keta* juveniles with different experimental feeding regimes and showed a direct linear effect on the mean width of daily increments. Similarly, Marshall and Parker (1982) presented data showing an increase in the relative size of otoliths of starved *O. keta* compared with that of fed controls, even though starvation had no effect on the number of increments. In contrast, Neilson and Geen (1985) found no effect due to ration alone on the thickness of increments in fry of *O. tshawytscha*, although an interactive effect due to ration level and water temperature was shown. These authors also found that increased feeding frequency significantly reduced mean increment width. Lastly, Campana (1984) found that increments of larval (<10 days old) *Porichthys notatus* were more irregularly spaced than in juveniles, as were the increments of fish exposed to a constant photoperiod environment. From these results, it is apparent that the effect of food ration on the width of daily increments is complex and is at present not well understood.

There is still some question concerning how close the coupling is between somatic and otolith growth rates (Brothers 1981; Bradford and Geen 1987). Over the entire lifespan, otolith length and FL typically are highly correlated (Templeman and Squires 1956; Blacker 1974). This situation could not arise were not the growth rates correlated over a similar scale. Still, in the most rigorous examination of the extent of rate coupling to date, Bradford and Geen (1987) found no correlation between the observed growth rates of individual *O. tshawytscha* fry and otolith increment widths over relatively short-term (7–15 d) intervals, although a good correlation over a 51 d interval was observed. These authors point to the relatively conservative character of otolith growth (Casselman 1983; Gutiérrez and Morales-Nin 1986) as the reason for short-term uncouplings between somatic and otolith growth rates.

In our study, otolith microstructure typical of daily increments was observed in the sagittae of gindai (Fig. 2). Daily growth increments were previously described and illustrated for congeneric species by Ralston and Miyamoto (1981, 1983), Brouard et al. (1984), and Radtke (1987). Likewise, we observed annual hyaline and opaque zonations, which have been reported in the hard parts (otoliths and vertebrae) of other lutjanids (Loubens 1978; Chen et al. 1984; Edwards 1985; Manooch 1987; Samuel et al. 1987). Still, of the 11 deep slope species (*Pristipomoides zonatus*, *P. auricilla*, *P. filamentosus*, *P. sieboldii*, *P. flavipinnis*, *Aphareus rutilans*, *Etelis coruscans*, *E. carbunculus*, *Lutjanus kasmira*, *Caranx lugubris*, and *Selar crumenophthalmus*) caught during the Marianas survey and whose otoliths were examined in some detail (Ralston and Williams 1988), only gindai displayed hyaline and opaque zonations, even though all species exhibited microstructure typical of daily growth increments. The absence of annuli in the otoliths of these other species is difficult to explain because many are congeners, most are confamilials, and all but one (*S. crumenophthalmus*) occupy the same general deepwater habitat where gindai are found. As a group, these fishes are exposed to virtually identical environmental conditions. Neither is the diet of gindai in the Marianas particularly distinctive (Parrish 1987).

In contrast to the situation in the Marianas, studies by Loubens (1978) in New Caledonia and Samuel et al. (1987) in the Persian Gulf document distinctive hyaline and opaque annuli in a wide variety of the taxa indigenous to these areas. Although the occurence of annuli in the otoliths of a variety of tropical and subtropical species is now well documented (Manooch 1987), our understanding of when and how they form is quite limited (see below).

Von Bertalanffy growth curves were developed for gindai by using both increment microstructure (Fig. 4) and annual marks. Likewise, the L_∞ parameter of the von Bertalanffy growth equation was estimated by using the regression method of Wetherall et al. (1987). Moreover, the analysis based on annual markings was tentatively validated with an abbreviated form of marginal increment analysis, wherein the seasonal presence or absence of opaque margins was established for the various pooled ring groups. A preferred approach is to measure the marginal increment for each ring group separately (e.g., Chen et al. 1984; Matheson et al. 1986). Although the importance of this type of validation has been overlooked (e.g., Beamish and McFarlane 1983), it is a very useful technique, especially in situations where capture is fatal.

A comparison of von Bertalanffy parameter estimates obtained by the three wholly independent approaches (increment microstructure, annuli, and length-frequency analysis) shows reasonable correspondence. The two estimates of growth coefficient (K) differed somewhat (0.234 versus 0.156 yr^{-1}), although estimates of L_∞ were substantially closer (442, 537, and 466 mm FL, respectively). Given that the annual marks were only weakly expressed, these findings support the conclusion that the microstructure observed in gindai otoliths (Fig. 2) results from the daily accretion of increments and, to the extent that annuli have been validated (Fig. 6), verifies the method of increment widths employed here. Likewise, the Monte Carlo simulation demonstrated that from an analytical point of view the method is free of significant bias.

The results obtained here were also compared to what we know of lutjanid growth by using the growth performance index developed by Munro and Pauly (1983) (see also Pauly and Munro 1983). For a specifically delimited taxon, this index empirically quantifies the well-known inverse correlation between K and L_∞ (Beverton and Holt 1959; Cushing 1968) and provides a simple basis for predicting K with an estimate of L_∞. Specifically, Manooch (1987) tabulated the results of growth studies covering 46 snapper and 31 grouper (Epinephelinae) stocks and calculated the combined growth performance regression for these taxa ($r^2 = 0.57$). With his equation, we predicted K by using each of our three estimates of L_∞ (see above). These calculations resulted in $K = 0.228$, 0.200, and 0.220 yr^{-1} for maximum sizes derived from daily increment microstructure, annuli, and length-frequency analysis, respectively. The estimates compare favorably with the value obtained solely from the study of otolith microstructure ($K = 0.234$ yr^{-1}), indicating that our results are in close agreement with existing information concerning lutjanid growth.

Calculating the age at first annulus formation provides additional evidence that the approach presented here is valid. The data presented in Table 3 indicate that the first annulus occurs at an otolith length of 3,117 μm. An estimate of age at this otolith length can be obtained from Table 2 by linear interpolation of the data falling in otolith length intervals 6 and 7; i.e., the otolith is 3,000 μm at age 0.6 and is 3,500 μm at age 0.8. This calculation indicates that the first annulus forms at an age of 0.65 year. Given that the opaque zone forms in January–February (Fig. 6), the predicted birth date by back-calculation is early June, in close agreement with observed spawning activity (Fig. 9). Moreover, the mean monthly sea surface temperature at Tanguisson Point, Guam, reaches its annual minimum during January–March (data for the period 1963–72 from Eldredge (1983)), suggesting that temperature fluctuation may be responsible for the formation of the annuli, although this species is found below the thermocline throughout the year (Eldredge 1983) and other closely related sympatric species lack zonations.

Some consideration of the underlying assumptions, advantages, and disadvantages of the method presented here is required. Without doubt, the most important assumption of the approach is that increments are deposited daily throughout the size range where increment width data are gathered. There is a substantial body of literature to show that interruptions to the daily increment record can occur (e.g., Geffen 1982, 1986; McGurk 1984; Jones 1986), especially in larger and older individuals (e.g., Pannella 1971; Ralston and Miyamoto 1983). Likewise, we know that with light microscopy the resolution of increments much less than 1.0 μm in width is physically impossible (Campana and Neilson 1985). This problem therefore becomes increasingly acute among the largest fish (see Table 2 and Figure 3). Together these findings have led to the view that daily growth increments are of little use in ageing large, old fish (Beamish and McFarlane 1987).

In this study, the deposition of daily increments became irregular at otolith lengths in excess of 7,500 μm. Beyond this length, the increments were also difficult to resolve microscopically due to small size. Consequently, no increment width data were collected at otolith lengths >7,500 μm. This corresponds to a FL of 329 mm (Fig. 1), which, although of a size that is reproductively competent (S. Ralston, unpubl. data), is smaller than most of the gindai caught during the field surveys (Fig. 7). Thus, the estimated von Bertalanffy curve presented here is largely based on back-calculated data obtained from the younger stages of growth. Nonetheless, we believe that daily increments can be useful in developing growth curves for use in stock assessments, even if data representing the older stages are not included in the analysis. This is especially true if the L_∞ parameter is estimated from length-frequency data (Fig. 8, Wetherall et al. 1987), avoiding the extrapolation problem described by Hirschhorn (1974). Still, validation of the increment periodicity assumption remains an essential component for future applications of the method.

Another assumption implicitly made is that no systematic bias was introduced into the estimation procedure by the manner in which sampling locations were chosen for measuring increment widths. For example, readings were made at specific points along the postrostral growth axis, i.e., where it was possible to distinguish the characteristic bipartite structure of daily increments. However, we also observed broad transition areas lacking in visually conspicuous microstructural features. If these ill-defined regions were elicited by periods of either fast or slow growth, then our estimates of mean otolith growth rate would be biased. To counter this we tried to representatively sample all daily increments (large and small) and we avoided measurements beyond 7,500 μm (see above). Still, we must assume that otolith growth rates calculated from regions where daily increments are visible are otherwise no different from regions where they are not.

Numerical integration of otolith growth rates provided a series of ordered pairs of age and otolith length. Otolith lengths were then converted to FL through regression analysis. The only FL data included in the nonlinear von Bertalanffy regression (Fig. 4), however, were based on otolith lengths in excess of 3,000 μm. Note that the excluded data (intervals 1-6) represent the first year's growth, i.e., the early life history. Although the von Bertalanffy growth equation has historically been the model of choice in stock-assessment applications, including especially the Beverton and Holt (1957) dynamic pool model, it provides a poor description of growth during the early life history. Inflected growth typically characterizes this stage, which is better fit with a Gompertz-type curve (Zweifel and Lasker 1976). By excluding ages <0.8 years from the von Bertalanffy regression analysis, we constrain the data used to estimate the model to the domain over which meaningful predictions are made. Moreover, predictions of FL based on otolith length are also obtained from regression analysis (Fig. 1). Because the smallest otolith used in developing the regression equation was 5,043 μm (see Figure 1), application of the equation to predict the FL of a fish whose otolith is less than this size represents an unnecessary extrapolation of the fitted model.

One of the side effects of deleting points from the early life history is to diminish the importance of weighting. Note that the statistical weights of the data used in the regression (Table 2) are very similar (coefficient of variation = 0.78%). Thus, although it may be desirable from a theoretical perspective, weighting had a negligible effect on the parameter estimates.

One of the principal advantages recommending this approach is an increase in efficiency and objectivity relative to studies that obtain complete counts of daily growth increments (Uchiyama and Struhsaker 1981; Brouard et al. 1984; Radtke 1987). Because all increments need not be visually conspicuous for a particular preparation to provide useful information, as is true of studies relying on whole counts, the observer can utilize only those portions of the otolith where the microstructure is clearly expressed. Enumeration of ill-defined increments in poorly developed regions of the otolith is avoided. This feature also makes it possible to automate the procedure (Casselman 1983; McGowen et al. 1987) and ultimately to realize the goal of standardizing age determinations (Boehlert and Yoklavich 1984; Boehlert 1985).

Powerful statistical tests of growth heterogeneity also are possible with the acquisition of increment width data (Table 1, Fig. 3). Evaluation of statistical differences in populations with respect to the parameters of the von Bertalanffy growth equation is cumbersome at best (Gallucci and Quinn 1979; Bernard 1981; Kappenman 1981). Analysis of covariance of increment width data provides a convenient and widely available means of testing for growth heterogeneity among any statistical populations of interest.

One of the principal disadvantages of the method outlined here is that growth variation among individuals within the sampled population is lost through averaging of the data. The final growth curve given in Figure 4 describes the mean growth of the sampled population of gindai. Of course, length variation at age is extremely important, and its description is required for application of the more powerful and realistic stock-assessment models, especially in cohort or virtual population analysis (Ricker 1975). Nonetheless, given the difficult conditions surrounding assessment work in tropical environments (Gulland 1982), the application of yield/recruit models is a significant step forward (Munro 1982; Pauly 1982). In conjunction with the analysis of length-frequency distributions, the method proposed here is well suited to help meet that need.

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8963

Trends in Fisheries for Swordfish in the Pacific Ocean

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The broadbill swordfish, *Xiphias gladius* (Fig. 1), is largely distinguishable from other billfishes by the absence of pelvic fins. It is a large pelagic species that attains a maximum size of 540 kg (1,190 lb) and is found in tropical, subtropical and temperate waters of the world's oceans and adjacent seas (Nakamura 1985, Palko et al 1981). It has been a favorite food fish in many countries since antiquity, esteemed for its white firm flesh, mild flavor, and high flesh-to-bone ratio.

Beside being esteemed as a food fish, the swordfish is a prized game fish. It is a difficult game fish to catch with rod and reel, so is pursued by only the most dedicated anglers. Trolling is the traditional method used, although this is done only after the swordfish is visually sighted basking at the surface.

In 1976, drift fishing for swordfish with baited lines and light sticks at night proved successful off Florida. This method quickly spread to other places along the Atlantic and Gulf of Mexico coasts of the United States (Palko et al *op. cit.).* The nominal sport catch, however, has remained small, amounting to no more than a few hundred swordfish per year.

The commercial fisheries produce more than 50,000 mt annually and are by far the major producers of swordfish. They are the focus of this chapter, which begins with a discussion of the markets, or forces that directly influence the level of commercial fishing for swordfish. This is followed by a review of the world catch and a description of the major fisheries in the Pacific Ocean, and concludes with a discussion of trends and outlook for the Pacific fisheries.

Global Markets

Commodity markets for swordfish are forces behind production. As a food fish having a high market value and ability to hold quality when frozen for long-distance shipment, swordfish is produced and traded on an international scale. It is sold fresh or frozen as steaks, fillets, and for raw consumption. The major markets are western Europe, Japan, and the U.S. Collectively, they account for an estimated 87% of the annual consumption.

Europe

The western European market is the largest, estimated to consume about 35% of the annual world supply of swordfish, principally for steaks and fillets. Consumption is concentrated in the Mediterranean countries, particularly Italy and Spain. This market depends largely on swordfish caught by the Spanish, Italian, and Greek fleets fishing on stocks in the Atlantic Ocean and Mediterranean Sea (ICCAT 1988).

Japan

The second largest market for swordfish is Japan. Consumption is estimated to be about 30% of the annual world supply. This market is primarily for high-quality fish, eaten raw as "sashmi" and "sushi." The product must be fresh or, if frozen, kept at low temperatures (−50° to −60°C, or −58° to −76°F) for retention of desired qualities. Average ex-vessel price was approximately $4.70/kg ($2.13/lb) in 1986 (Yao 1988).

A world-wide Japanese fleet of longliners is largely the source of fish for this market. About 70% to 80% of the supply is from swordfish stocks in the Pacific Ocean and the remainder is evenly divided from stocks in the Atlantic and Indian oceans.

United States

The U.S. market currently consumes about

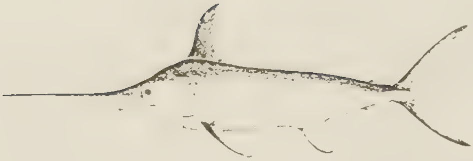

Figure 1. Broadbill swordfish with distinguishing characteristics, including absence of pelvic fins (from Nakamura 1985).

12,000 mt annually, or 22% of the world supply of swordfish. Products are in the form of fresh and frozen steaks and fillets. This market is growing at an estimated annual rate of 5% to 7% (Lipton 1986).

About half of the U.S. supply comes from the U.S. fleet and half from foreign fleets operating in the Atlantic and Pacific oceans. Canada, Spain, and Taiwan currently are the major sources for U.S. imports. In 1986, the average ex-vessel price for U.S.-caught swordfish was $6.95/kg ($3.15/lb); for foreign-caught fish, it was $5.65/kg ($2.56/lb).

The U.S. market has evolved in phases. Before 1971, the market was almost completely dependent on imports, mainly from Canada and Japan (Fig. 2). The discovery in 1970 of high levels of mercury residue in swordfish steaks (Peterson et al 1973), in excess of established health safety margins, reversed this picture.

In 1971, the U.S. strictly enforced a regulation on the permissible level (0.5 ppm) of mercury in imported fish. Consumers stopped buying swordfish, supplies quickly dried up and the market collapsed (Lipton *op. cit.*). A slow recovery began in 1973, with U.S. consumers cautiously returning to the market as fears of mercury poisoning faded. U.S. fishermen increased their efforts to fill the supply lines since they were largely exempt from the mercury regulation that had virtually stopped the entry of imports. They captured over 90% of the market and began establishing new fisheries to meet the increasing demand. Production increased slowly at first, and grew. By 1978, it had grown sufficiently to attain the levels that were consumed before the mercury scare of 1971, and was increasing in line with renewed market growth. In 1985, however, domestic production showed signs of leveling off at 7,500 mt (Fig. 2).

In 1979 the mercury regulation was revised to allow a higher level of 1.0 ppm. In combination with rising value of the dollar relative to foreign currencies and, foremost, exponential growth in U.S. consumption of swordfish, this revision allowed imports to be more competitive (Lipton *op. cit.*). Significant amounts of foreign-caught swordfish began reappearing in 1981. Imports captured 10% of the market share that year and grew in subsequent years. The largest increase occurred in 1985, when domestic production leveled off while consumption continued upwards. Imports captured 35% of the market in 1985, increasing further to 44% in 1986.

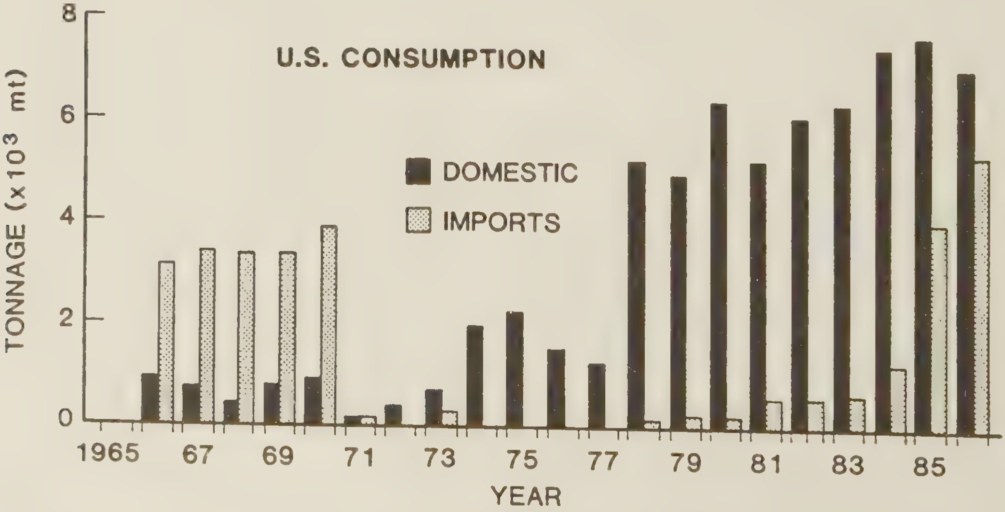

Figure 2. Tonnage of swordfish consumed by U.S. consumers, 1966-1986. (Source: Lipton 1986 and NMFS.)

Global Production

Identifying trends in the catch of swordfish on a world-wide basis is difficult, owing to changes in data gathering and reporting procedures over time, inaccurate reporting of some statistics, and non-reporting for some fisheries. Nonetheless, by piecing together recent estimates from several sources, particularly from ICCAT *(op. cit.)* and FAO (ms), the global catch appears to be increasing — from a low of about 27,000 mt in 1972 to a high of approximately 56,000 mt in 1986.

The major increases have been in the Atlantic Ocean and Mediterranean Sea although the trend has also been upward in the Pacific Ocean. In 1972, the Pacific catch was 12,600 mt or about 47% of the total global catch; in 1986, it was about 21,000 mt and only 37% of the global catch (Fig. 3).

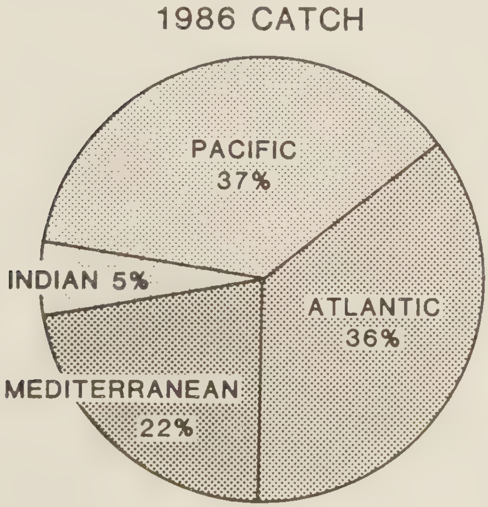

Figure 3. Proportion of swordfish catch by ocean, 1986.

The Pacific catch has shown an increasing trend since 1972, although remaining below the peak of 24,300 mt recorded in 1961 (Fig. 4). The stocks are considered to be in good condition (Bartoo and Coan 1989) and able to sustain increased catches. Comparison of Pacific catches with those of the Atlantic or Mediterranean, and relative sizes of the areas where they are made, suggest that there is considerable opportunity for increased production of swordfish from the Pacific Ocean.

Nations participating in the Pacific fisheries include: United States (harpoon and drift gillnet fisheries off California); Chile, Mexico, and Peru (coastal handline, gillnet and longline fisheries); Japan (Pacific-wide longline fishery and a coastal, mainly drift gillnet fishery off Honshu); the Philippines (coastal handline fisheries); Taiwan (Pacific-wide longline fishery and coastal, primarily longline and harpoon fisheries); and Republic of Korea (Pacific-wide longline fishery).

Pacific Fisheries

The geographic distribution of swordfish varies with seasonal changes in water temperature, but can extend from 50°N lat to 50°S lat. Preferred water temperature for swordfish is 18° to 22°C (64° to 72°F) (Nakamura *op. cit.)* and varies with size of the animal. Juveniles prefer warm water and are found only in the tropical region. Adults have a wider temperature tolerance and occupy the full distributional range, spawning in the tropics and feeding in the temperate regions. Females reach a larger maximum size than males, and can tolerate colder water and occupy the highest latitudes. The smaller adult males generally remain in warmer water close to the equator.

Adult swordfish are found throughout the year in most parts of their distributional range, except in the extreme sub-polar latitudes during the winter. They concentrate in areas where food is abundant, commonly along frontal zones where ocean currents or water masses intersect to create turbulence and sharp gradients of temperature and salinity. The fisheries for swordfish occur in these regions of frontal zones.

In the Pacific Ocean, there are five frontal zones (Sverdrup et al 1942) where swordfish are found in fishable concentrations (Fig. 5): (1) in the northwestern Pacific (Huang 1974, Sakagawa and Bell 1980), where the warm Kuroshiro Current meets the coastal waters of Taiwan and Japan, and where the Kuroshiro Extension Current meets the Oyashio Current to the north; (2) off southeastern Australia (Sakagawa and Bell *op. cit.*), where the warm East Australian Current meets intrusions of the cold Southern West Wind Drift Current; (3) off northern New Zealand (Bailey and Ross 1987), where the warm South Equatorial Current intersects with intrusions of the cold Southern West Wind Drift Current; (4) in the eastern tropical Pacific (Squire and Au 1989), where the warm

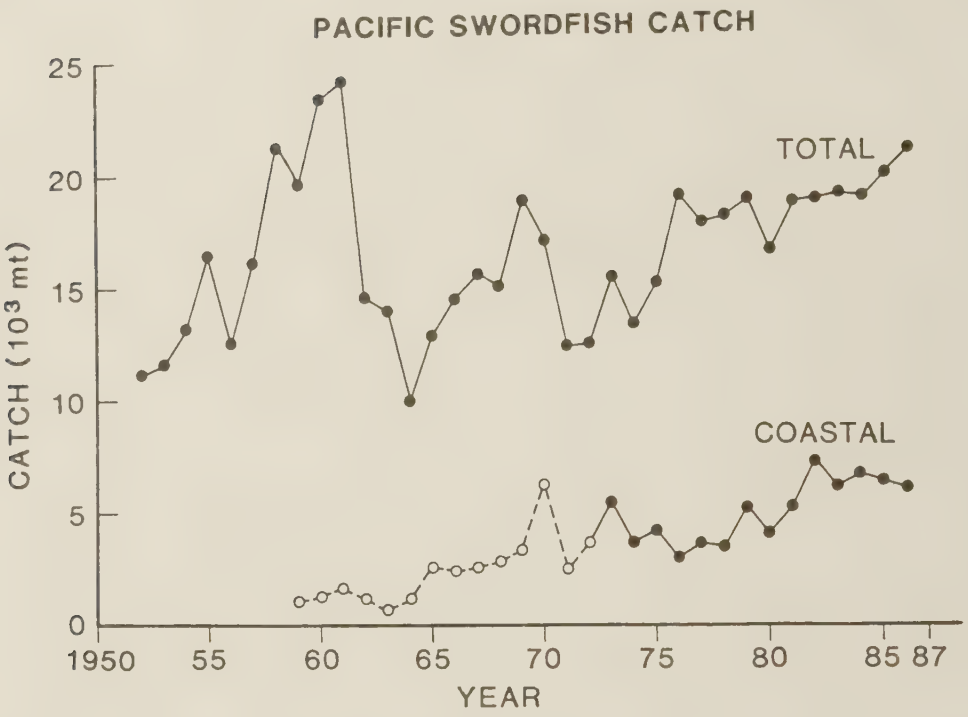

Figure 4. Total catch of swordfish from the Pacific Ocean, 1952-1987. Catches by gears, such as harpoon, drift gillnet, and longlines in coastal waters are labeled "coastal". High seas longline catches are not labeled. Open circles are estimated catches. (Source: FAO ms.)

Equatorial Counter Current intersects with the colder Peru Current: and (5) along Baja California, Mexico, and California, U.S.A. (Bedford and Hagerman 1983, Squire and Au 1989), where the cool offshore California Current intersects with intrusions along the coast of warmer water from the south.

Swordfish are caught in artisanal and other small-scale fisheries but mostly by fisheries that are large-scale commercial operations. Because swordfish forage in the surface waters during the night, inhabiting deeper depths during the day (Carey ms), catches are made principally during the night. Most of the Pacific catch of swordfish is taken incidental to fishing for other species, such as tunas, which are fished during the day. Typically, fisheries that catch significant quantities of swordfish, even incidentally as a complex of target species, are arbitrarily designated as swordfish fisheries.

This review, employed this procedure and applied it to the fisheries of Japan, Taiwan, and the U.S. The fisheries were further separated by major gear: longline, drift gillnet, and harpoon.

Japanese Fisheries

The Japanese fisheries, with total production of 14,300 mt in 1986, or 68% of the total Pacific production, are by far the most important in the Pacific Ocean. The fisheries can be separated into longline, drift gillnet, and harpoon. Each is actively managed by the Japanese government through a complex system of vessel licenses, gear limitations, and area-time regulations to reduce gear conflicts and to enhance economic viability of the fisheries. Over the years 1972 and 1985, the contribution of each fishery to the total catch has changed, with the drift gillnet fishery contributing a greater proportion, and the longline and harpoon fisheries contributing smaller proportions (Fig. 6).

Longline Fishery

The Japanese longline fishery is conducted

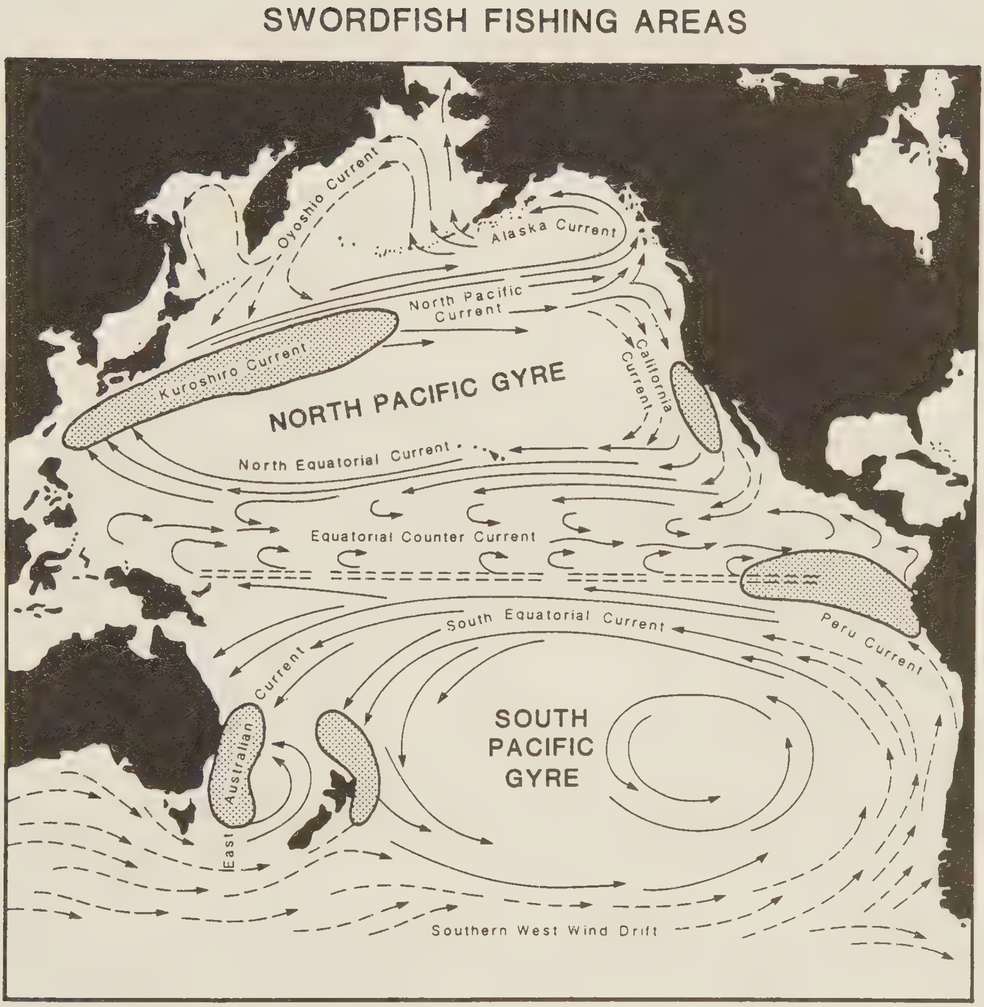

Figure 5. Location of major swordfish areas (stippled) in the Pacific Ocean. The areas correspond to zones of high production of food organisms and where major ocean currents meet.

on the high-seas using vessels of 50+ gross tons and in near-shore and coastal waters of Japan using vessels of less than 50 gross tons. The fleet consists of approximately 1,200 vessels of which about 600 may be deployed in the Pacific during a single fishing season.

The gear used by the vessels is the longline, consisting basically of a main line with float lines and branch lines with baited hooks. For the large high-seas vessels, the main line is set over a distance of 25-75 km (14-40 nmi) and fishes about 2,000 hooks during a single set.

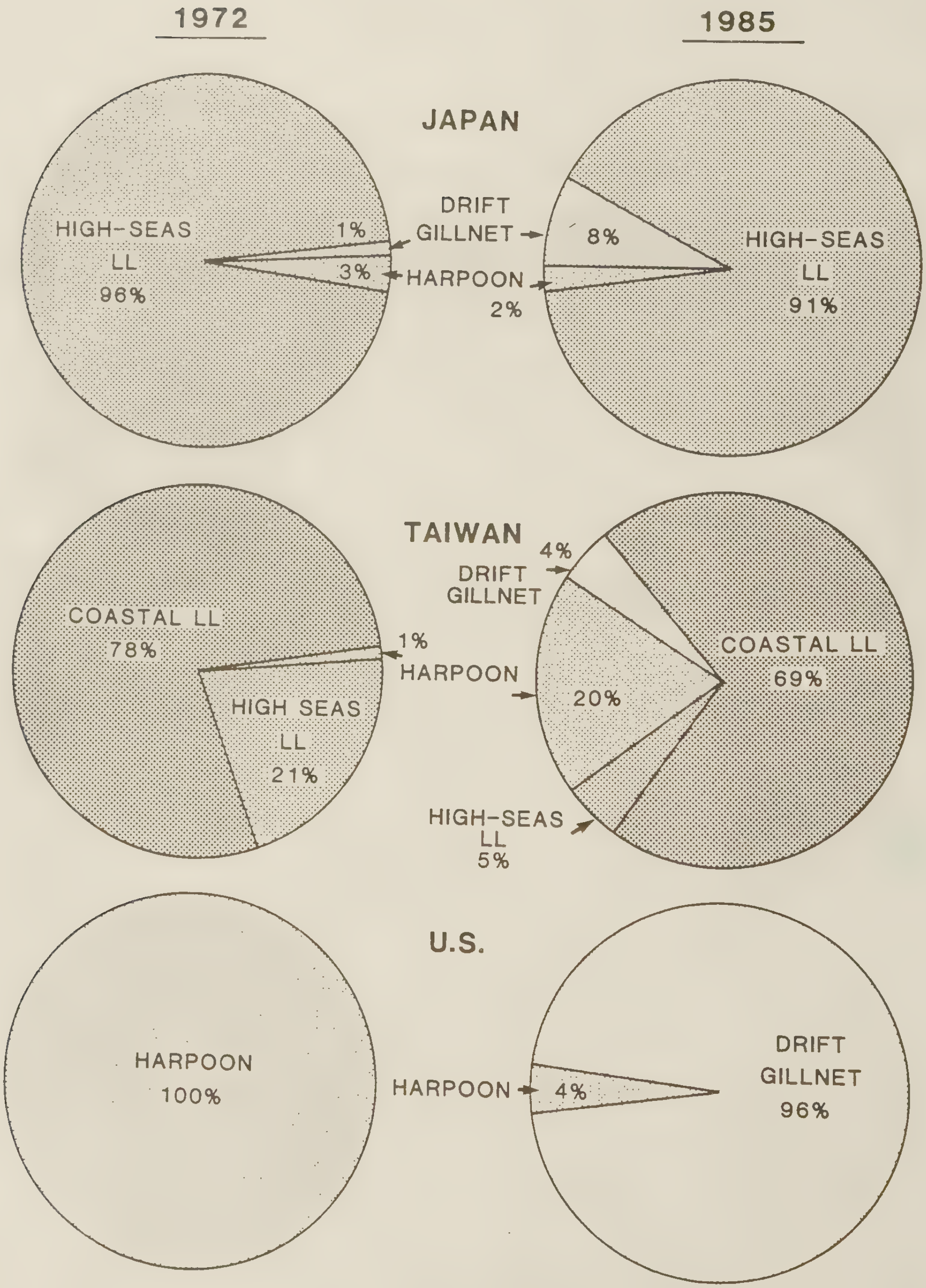

Figure 6. Comparison of percent swordfish catch by fisheries for 1972 and 1985.

Float lines are attached to the main line to regulate fishing depth, a maximum of 170 m (557 ft) for standard sets and about 300 m (984 ft) for deep sets (deep longlining). A set is normally deployed early in the morning and retrieved beginning around noon, frequently ending after midnight (Ueyanagi 1974).

Deep longlining is a relatively recent innovation that was introduced to catch the deep-swimming bigeye tuna, *(Thunnus obesus)*. Deployment started by the Japanese in about 1974 in the equatorial regions of the Pacific and Indian oceans (Suzuki et al 1977, Suzuki and Kume 1982). It spread gradually to all oceans and to other longline fleets, i.e., those of Korea and Taiwan. Because it fishes deeper, deep longlining is less efficient in catching the more shallow-swimming species — albacore *(T. alalunga)*, yellowfin tuna, *(T. albacares)*, and swordfish — than is the standard longline gear. The incidental catches of swordfish by this latter gear are probably largely made as the gear is being retrieved during the night hours.

Swordfish is not currently the primary target species of this fishery and the catch is a small proportion of the total longline catch (less than 5%). Tunas are the target species and the catch amounted to about 190,000 mt in 1986 (Sakagawa et al 1987). In past years, this was not the case as swordfish was a target species in certain areas of the Pacific Ocean and made up more than 50% of the catch in some 5 × 5 degree fishing areas (Bartoo and Coan 1989). In recent years, some vessels continue to target on billfishes, such as striped marlin *(Tetrapturus audax)*, and/or swordfish in limited areas off Mexico (Squire and Au 1989), New Zealand (Bailey and Ross *op. cit.)*, and in the Kuroshio Extension Current (Bartoo and Coan 1989).

During the period 1952 through about 1962, swordfish were specifically targeted, along with albacore, by the Japanese longline fleet. Night fishing at shallow depths with squid as bait was used in certain areas (Ueyanagi *op. cit.)*. The longline catch during that period reached a record high of 22,000 mt of swordfish in 1961 (Fig. 7). Since then the fishery changed to primarily day operations, using a mixture of bait types and emphasizing catching tunas for the sashimi market; swordfish catches slipped to a lower level, averaging 12,300 mt (1966-1969). In 1971, catches decreased again owing to the mercury scare and collapse of the U.S. market. Since 1975, catches have rebounded to an average of about 11,000 mt (Fig. 7).

The areal distribution of the swordfish catches for 1976 shows that swordfish were taken mostly in the northwestern region, along the edge of the Kuroshio and Kuroshio Extension Currents, off the Mexican coast, and off southeastern Australia (Fig. 8, panel B). In 1980, fishing effort was more widely distributed and for the most part targeted for bigeye tuna (Fig. 8, panel A). Significant amounts of swordfish continue to be taken in the northwestern region and in other areas where major frontal systems are located (Fig. 8, panel C). The eastern tropical Pacific, in particular, shows significant recent catches by this fishery.

Drift Gillnet Fishery

The Japanese drift gillnet fishery lands swordfish as a by-catch of fishing for other pelagic species in the northwestern Pacific Ocean. More than 1,600 vessels of varied sizes, 10 to 250 gross tons, participate in this fishery (Yonemori and Honma ms). Generally, the larger vessels operate on the high-seas and target pelagic species such as squid *(Ommastrephes bartrami)*, salmon *(Oncorhynchus* sp.), pomfret *(Brama japonica)*, and albacore. The smaller vessels operate closer to the coast off northern Honshu Island, primarily from July to October, and switch to other fisheries during the off-season (Anon 1978). This coastal component targets primarily striped marlin but also catches yellowfin tuna, skipjack tuna *(Katsuwonus pelamis)*, mahimahi (i.e., dolphin, *Coryphaena hippurus)*, sharks and swordfish (Anon *op. cit.)*. Fishing success of this fleet is largely dependent on oceanographic conditions associated with the meandering of the Kuroshio Current off Japan.

The gear used is multifilament netting of about 9 m (30 ft) deep and 18 cm (7 in) mesh size (Yonemori and Honma ms). The net is fished at the surface and a set can extend up to 12 km (6.5 nmi). Sets are usually made in the afternoon, allowed to drift during the night, and retrieved beginning before dawn.

This fishery began recording significant catches of swordfish in the mid-1970s (Fig. 7). Catches increased sharply to a peak of 3,500 mt in 1976, declined to 1,000 mt in 1979 and remained fairly level since then.

Harpoon Fishery

The Japanese harpoon fishery targets striped marlin and takes blue marlin *(Makaira nigri-*

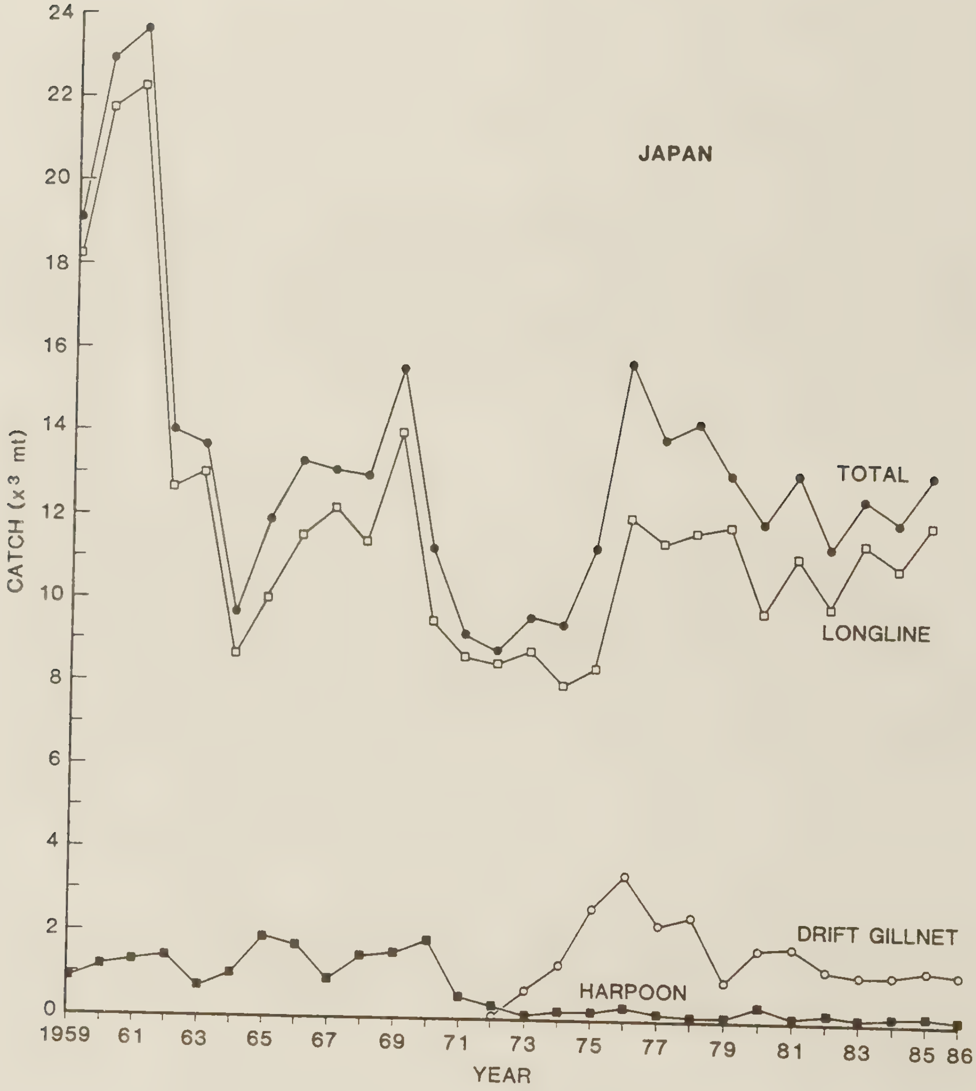

Figure 7. Catch of swordfish by gear for the Japaneses fisheries, 1959-1986. (Sources: FAO ms, Y. Watanabe pers. comm.)

cans), and swordfish incidentally. Because fishing with harpoons requires calm seas for visually sighting the basking fish, and for positioning the vessel within striking distance of the fish, oceanographic conditions, particularly associated with the Kuroshio Current, dictate the fishing season (Sawadaishi 1985). Typically, this fishery is active from December to May. The fishing areas are in the Bonin and Izu Islands (south of Tokyo) and off the northern coast of Honshu Island (off Miyako).

About 100 boats of less than 20 gross tons (mainly 3 to 15 gross tons) participate in this fishery. Most boats are active in harpooning only during December to May, squid jig fishing during the rest of the year (Y. Watanabe pers. comm.).

The gear used is a three-prong electric-dart

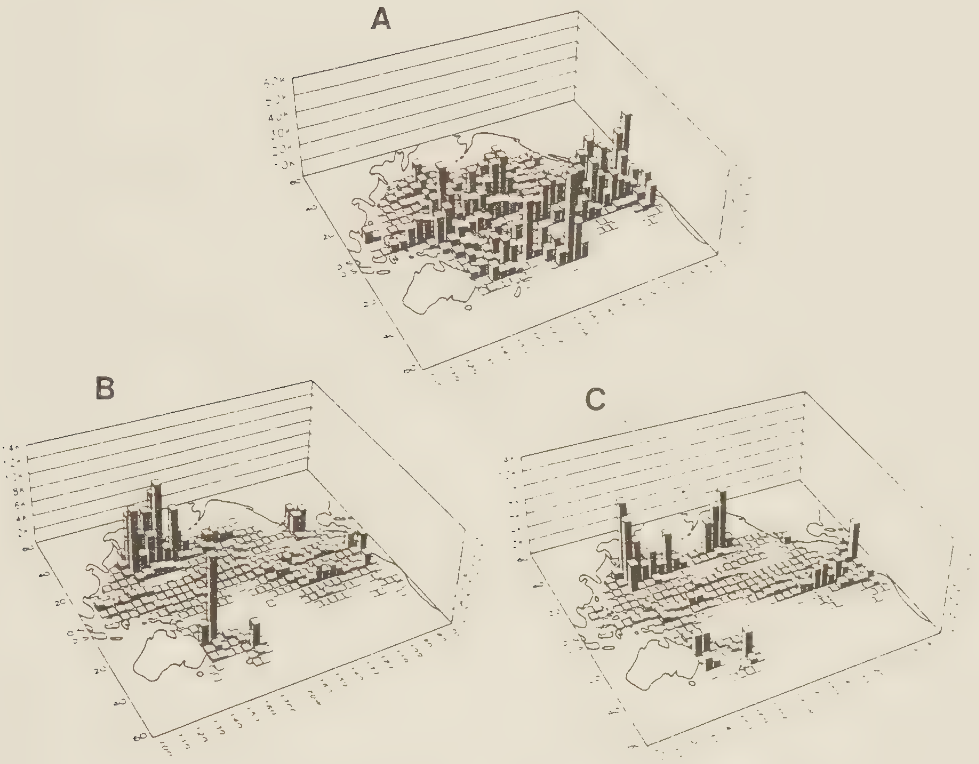

Figure 8. Areal distribution of catches (in numbers) for the Japanese longline fishery in the Pacific Ocean. Panel A is catches of bigeye tuna, the principal target species for 1980. Panel B is catches of swordfish for 1976, a year of exceptional high catches. Panel C is catches of swordfish for 1980, a recent year.

harpoon (Sawadaishi *op. cit.*). The pole is 5 m (16 ft) long and 4 cm (1.6 in) in diameter, of oak or reinforced plastic. Fastened to the tip of the pole is a steel attachment with three prongs, each holding a removable dart. The dart is 8 to 12 cm (3.1 to 4.7 in) long, arrow shaped and made of steel. Holes in the shank of the dart allow attachment of electrical wiring and the main line of 4 to 5 mm (0.16 to 0.2 in) diameter rope. The opposite end of the electrical wire is attached to a storage battery located in the engine room of the vessel.

Operationally, fish are sighted from the crow's nest. The vessel maneuvers to the target, and the harpooner on the bow plank is positioned. The harpooner throws the harpoon by hand. The harpoon tips embed in the fish and separate from the pole while the main line, with electrical wire, is played out as the fish tries to escape. The electrical shock is administered and the dead fish is retrieved.

The swordfish catch of this fishery ranged from a high of 1,700 mt in 1970 to a low of about 100 mt in 1986 (Fig. 7). In 1971, the catch fell substantially (−71%) and has not recovered. Because this low catch corresponds to the period of increased activity of the drift gillnet fishery, the harpoon fishery appears to compete directly with the drift gillnet fishery for available swordfish in the coastal waters.

Taiwanese Fisheries

Taiwanese fisheries contributed an estimated 700 mt, or 3% to the total Pacific swordfish catch in 1986. They are not major fisheries, but are reviewed here because Taiwan is a major exporter of swordfish to the U.S. market and Taiwan has a major world-wide longline fleet. Taiwanese fisheries that catch significant amounts of swordfish are the high-seas longline, coastal longline, and harpoon fisheries.

Between 1972 and 1985, the contribution of each of these fisheries to the total Taiwan catch of swordfish changed markedly. Most significant has been the decreased percentage contribution by the longline fisheries and increased percentages by the harpoon fishery and by the emerging drift gillnet fishery (Fig. 6). Swordfish catches in this latter fishery are not yet large enough to be considered significant.

High-Seas Longline Fishery

The high-seas longline fleet of Taiwan consists of vessels larger than 50 gross tons. This fleet numbered more than 200 vessels in the Pacific in the 1970s, but have been reduced to fewer than 100 in 1984. Fishing effort (number of hooks) for this fleet likewise decreased by 80% between 1980 and 1985 (Tuna Research Center 1986).

Like the Japanese longline fleet, the Taiwanese vessels operate on the high-seas in pursuit of large tunas. Albacore is the principal target species (Sakagawa et al *op cit.*), making up 88% of the tuna catch of 7,000 mt in 1985. Recently, modern longliners have been added to this fleet for catching large tunas, principally yellowfin and bigeye, for the Japanese sashimi market.

Swordfish is an incidental species caught by the vessels. The catch has been less than 300 mt and, since 1980, it has decreased to a low level of 40 mt in 1985 (Fig. 9). Catches have been small because fishing is principally in the southwestern region of the Pacific and for albacore (Fig. 10). The area fished also appears to have a low density of swordfish. Highest catches of swordfish occur off southeastern Australia and northern New Zealand.

Coastal Longline Fishery

Taiwan has a large number of longline vessels (2,080 registered in 1986) that fish the nearshore and coastal waters of Taiwan. Most are of 20 to 50 gross tons and operate off eastern Taiwan along the edge of the Kuroshio Current in pursuit of large tunas (Huang *op. cit.*). This

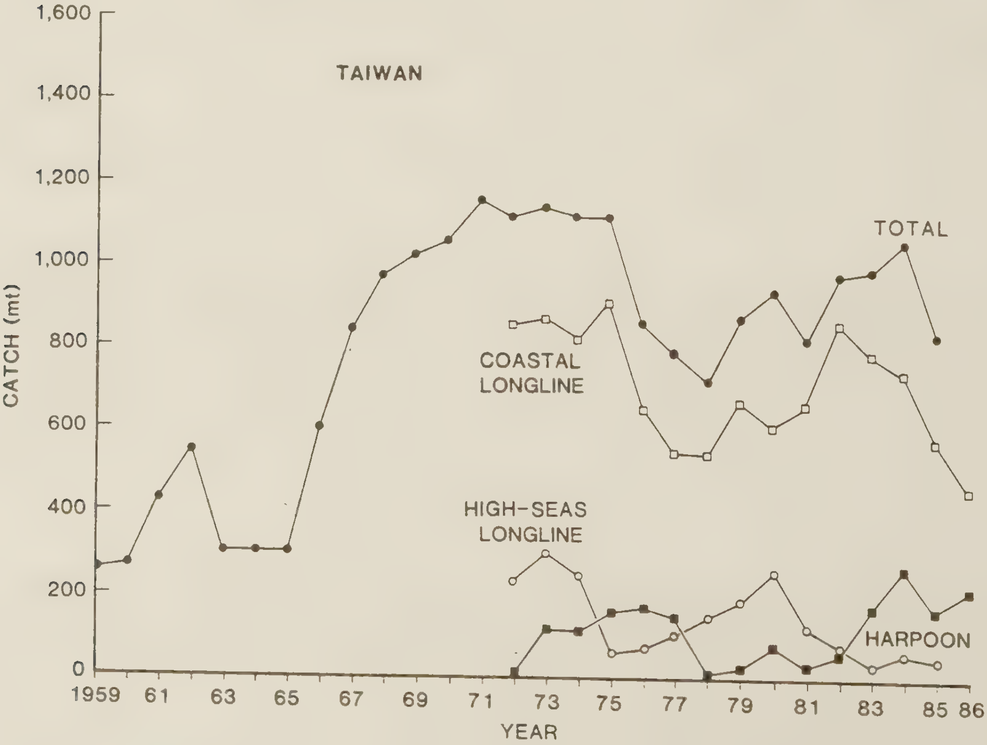

Figure 9. Catch of swordfish by gear for the Taiwanese fisheries, 1959-1986. (Sources: Tuna Research Center 1986, FAO ms. H.C. Liu, pers. comm.)

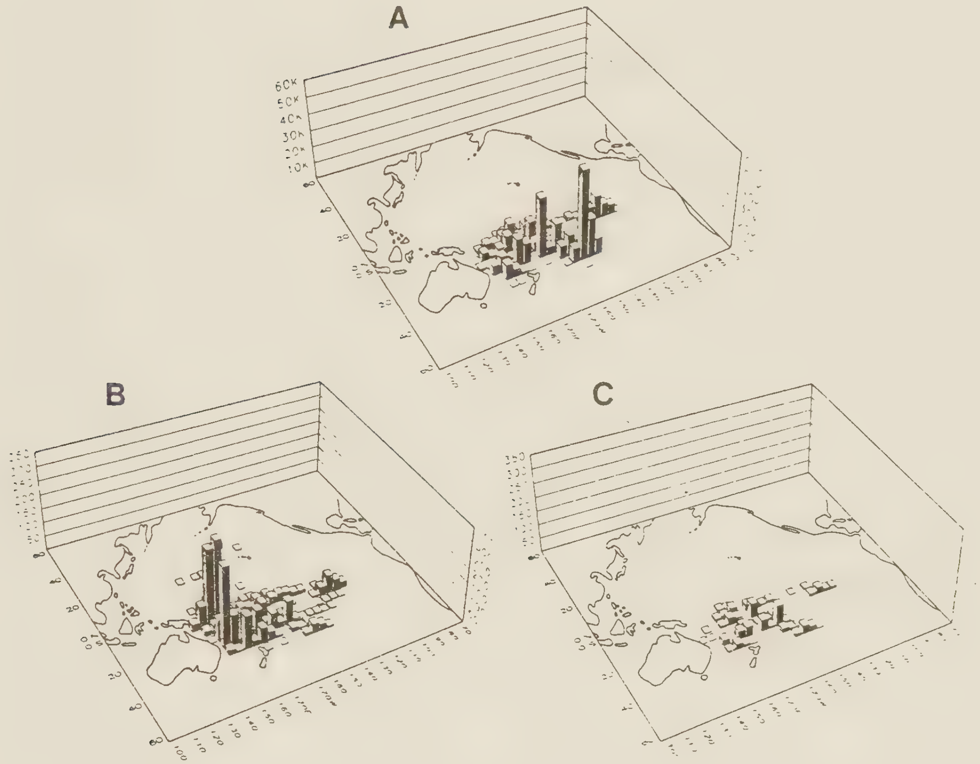

Figure 10. Areal distribution of catches (in numbers) for the Taiwanese longline fishery in the Pacific Ocean. Panel A is catches of albacore, the principal target species for 1985. Panel B is catches of swordfish for 1977, a year of exceptionally high catches. Panel C is catches of swordfish for 1985, a recent year.

fleet catches significant amounts of billfishes, including swordfish, and other large pelagic species as a by-catch.

The swordfish catch of this coastal longline fishery has fluctuated between 500 mt and 900 mt (Fig. 9). Since 1982, the trend has been downward, with the catch reaching a record low of 500 mt in 1986. Among the billfishes caught in this fishery, swordfish ranks low at 14%, behind blue marlin at 35%, and sailfish *(Istiophorus platypterus)* at 24% (Table 1).

Harpoon Fishery

Harpoon fishing for billfishes was introduced into Taiwan by the Japanese in 1913 (Huang *op. cit.)*. In 1986, a total of 390 vessels participated in this fishery. They operated primarily in the eastern region of Taiwan, from the southern ports of Kaohsiung and Taitung and from the northern port of Keelung.

Unlike the Japanese harpoon fishery, this fishery appears to target a complex of billfishes, with swordfish ranking low (Table 1). Blue marlin, sailfish, and black marlin *(Makaira indica)* are principal target species. Catches of swordfish were low during 1978-1982, at less than 100 mt annually (Fig. 9). Since then, it appears to have stabilized at the 200 mt level.

Table 1. Average (1980-1985) catches of billfishes by species in the billfish catch of Taiwanese fisheries. (Source: H.C. Liu pers. comm.)

	Billfish species					
Fishery	**Swordfish**	**Striped marlin**	**Blue marlin**	**Black marlin**	**Sailfish (others)**	**Total**
High-seas longline						
Catch (mt)	94	145	236	19	15	509
Percentage	18	29	46	4	3	100
Coastal longline						
Catch (mt)	699	524	1,695	773	1,144	4,835
Percentage	14	11	35	16	24	100
Harpoon						
Catch (mt)	120	147	585	524	554	1,930
Percentage	6	8	30	27	29	100
Total						
Catch (mt)	913	816	2,516	1,316	1,713	7,274
Percentage	12	11	35	18	24	100

United States Fisheries

U.S. fisheries for Pacific swordfish are centered in the coastal waters off southern California. In 1986, the fisheries produced about 2,100 mt of swordfish, representing 10% of the total swordfish catch from the Pacific. Management of the fisheries is largely by state agencies through limits on number of fishing licenses, design of the gear, and fishing season and area (Squire ms).

The U.S. fisheries can be divided into two: drift gillnet and harpoon. The drift gillnet fishery is relatively new, started in the late 1970s. It currently is the dominant fishery (Fig. 6). The harpoon fishery, in contrast, dates back to the turn of the century (Bedford and Hagerman *op. cit.*) and is on the decline.

Drift Gillnet Fishery

During 1977 and 1978, southern California fishermen discovered that drift gillnets set for common thresher shark *(Alopias vulpinus)* and shortfin mako *(Isurus oxyrinchus)*, resulted in incidental catches of the more valuable swordfish. This discovery, along with development of a market for fresh shark fillets, led to rapid improvements in the gear and in the number of fishermen using the gear; many were swordfish harpoon fishermen, as well. By 1980, a full-fledged modern drift gillnet fishery targeting sharks, with significant catches of swordfish, was in operation.

Opposition mounted to this new fishery (Herrick and Hanan 1988). Opposition forces were concerned with the adverse effects on other commercial and recreational fisheries as well as protection of marine mammals and seabirds that get entangled in the gear. As a result, a series of laws was enacted by California to control the drift gillnet and other similar net fisheries.

Most significant of the new laws was one requiring revocable, nontransferable permits for all drift gillnet fishermen, and which specified qualifications for obtaining them. It also required permit holders to submit logbooks and to allow observers on fishing trips.

Another significant piece of legislation was passed in 1982 in recognition of the significant amounts of swordfish taken in drift gillnets and concern over excessive effort on the shark resource (Herrick and Hanan *op. cit.*). The legislation allowed for targeting swordfish with drift gillnets and placed a limit on number of licenses. This transformed the fishery overnight. Swordfish became the target species and sharks the secondary species. A target of no more than 150 permits was put into effect (Herrick and Hanan *op. cit.*). Because there were about 200 fishermen with drift gillnet gear at that time, all were issued permits and a moratorium placed on new issues until the number drops below 150. Since then, the number has remained relatively stable at about 200 to 225 permits (Fig. 11).

The drift gillnet used is constructed of nylon twine and with large mesh, 20.3 to 50.8 cm (8 to 20 in) (Bedford and Hagerman *op. cit.*). It is approximately 18 to 37 m (60 to 120 ft) deep and 1,829 m (6,000 ft) long. It is fished at night one meter to 2.7 m (3 to 9 ft) beneath the surface. Fishing depth is controlled by suspended float lines at about 18 m (60 ft) intervals along the length of the net. The net drifts with one end attached to the vessel and the other attached to a buoy, which contains a strobe light and radar reflector.

Before 1982, the U.S. drift gillnet fishery operated in an area south of Point Conception, California, to the Mexican border and within about 92 km (50 nmi) of the coast (Fig. 12). This is the same fishing area used by the older harpoon fishery for swordfish. Beginning in 1982, the fishery expanded northward about to San Francisco and, in some years, even farther northward to waters off Oregon and Washington (Fig. 13). Fishing in the most northern part is almost exclusively for sharks and only rarely results in swordfish catches; hence, swordfish fishing by the fleet can be considered limited to waters off California.

The fishing season is regulated and extends from May to February. Within this season, the distribution of fishing effort is bimodal, May and October (Fig. 14). Approximately 80% of the fishing takes place, however, during August through January, when 99% of the catch is made.

Most of the catch (75%) is made in the area south of Point Conception, with exceptional catches made off San Diego, between Catalina Island and the mainland (off Los Angeles), and southeast of Anacapa Island in the Santa Barbara Channel Islands (Fig. 15). North of Point Conception, the catch is relatively small (about 6,000 fish in the 1984-1985 season) and there is only one exceptionally high catch area, off San Francisco. Fishing effort is also reduced in this northern area owing to poor ocean condi-

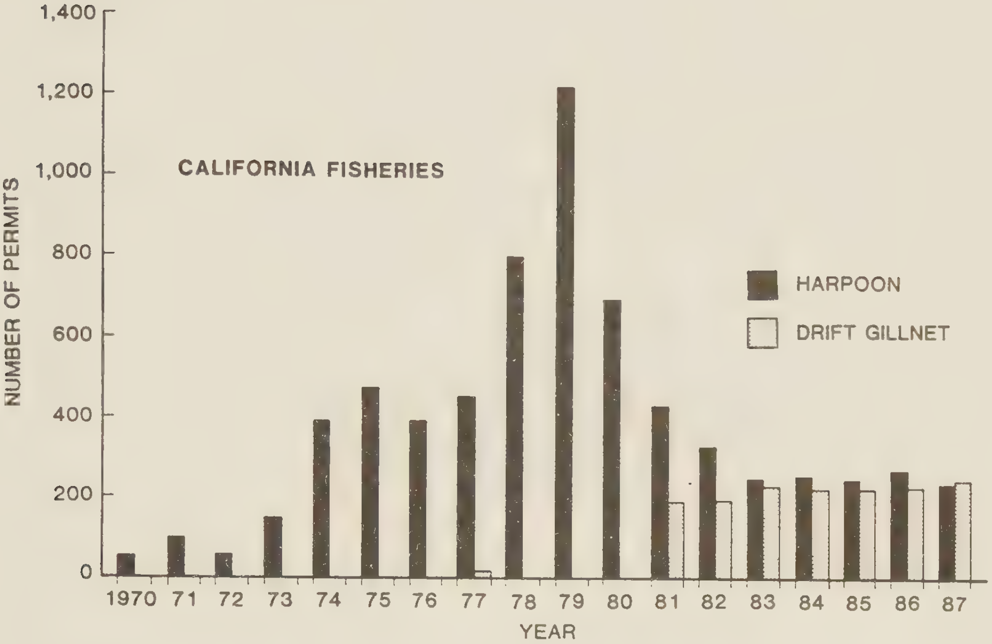

Figure 11. Number of permits issued by California for fishing with harpoon and drift gillnet.

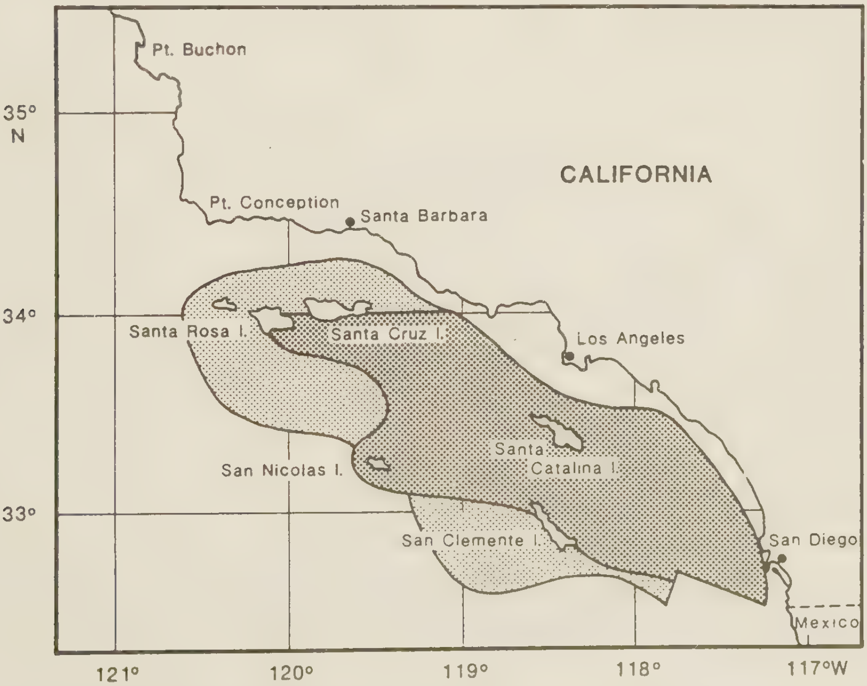

Figure 12. Location of fishing areas of the U.S. harpoon fishery (dark stipple) and drift gillnet fishery (light stipple) for swordfish off California.

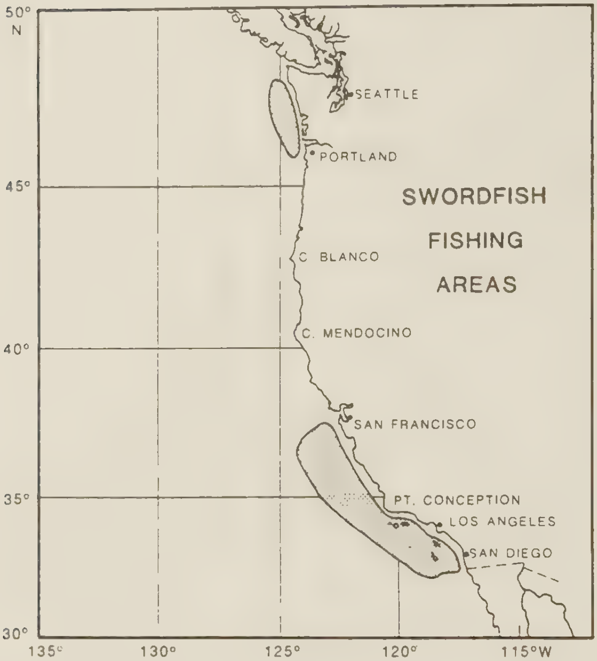

Figure 13. Location of fishing areas (stippled) of the U.S. drift gillnet fishery for swordfish and sharks.

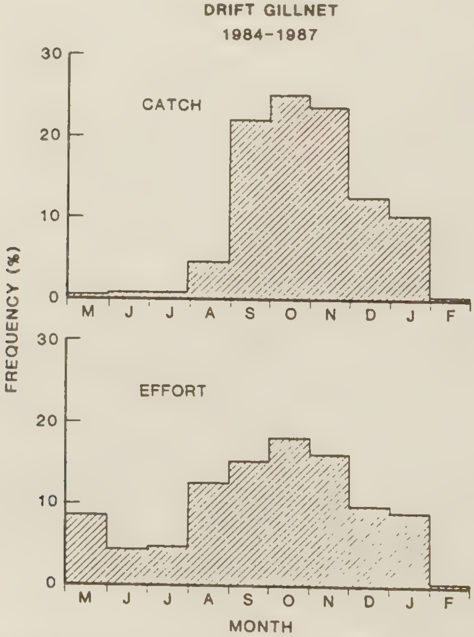

Figure 14. Seasonal distribution of swordfish catch and fishing effort for the U.S. drift gillnet fishery. (Source: D. Bedford pers. comm.)

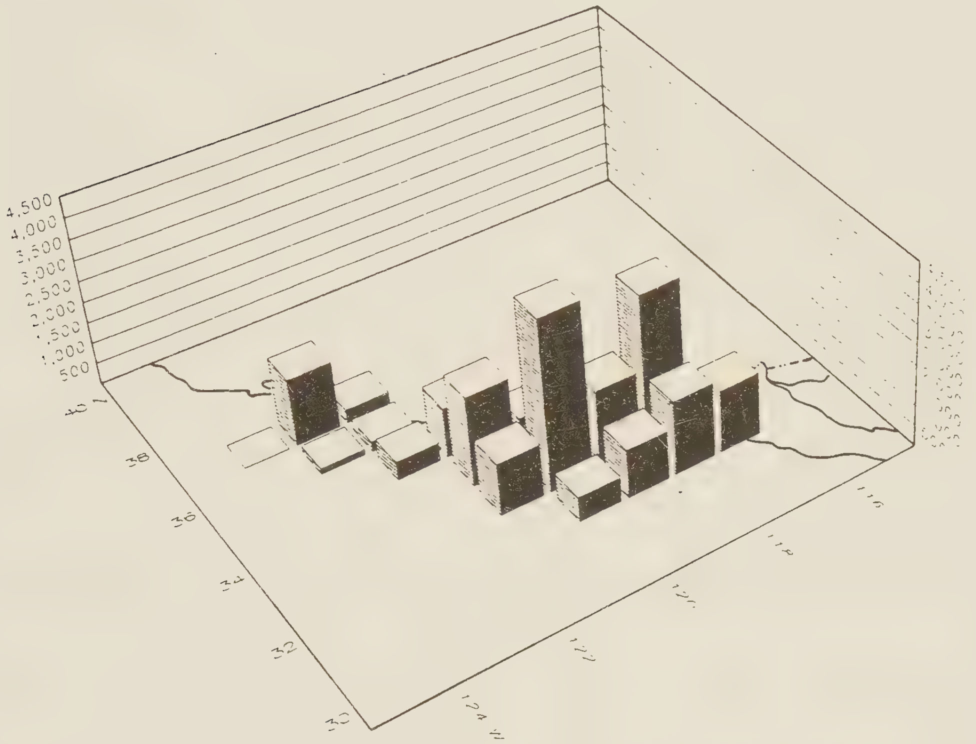

Figure 15. Areal distribution of swordfish catches (in numbers) for the U.S. drift gillnet fishery off California, 1985.

tions and weather for drift gillnet fishing during most of the fishing season (Bedford and Hagerman *op. cit.*).

The total catch in this fishery increased steadily from 1980 to 1985, recording an impressive 890% increase (Fig. 16). Since then, the catch has fallen sharply to 1,900 mt in 1986 and to 1,400 mt in 1987, despite stable fishing effort of approximately 10,000 days fished per season. The average size of fish caught has not been affected and has remained stable[1].

Harpoon Fishery

The oldest U.S. fishery for Pacific swordfish is the harpoon fishery off California. The fishery began at the turn of the century and grew in response to consumer demand for swordfish. It is exclusively devoted to catching swordfish during a season that extends from about June to December and peaks in August or September (Fig. 17).

The heyday for this fishery was in the 1970s. The U.S. mercury regulation cut off foreign supplies and prices rose. This encouraged participation and innovation in the fishery. One innovation was the use of airplanes to locate swordfish more efficiently, and for directing the harpoon vessel. This innovation proved so successful that a flood tide of new participants entered the fishery and as many as 20 airplanes were engaged full time by the fleet (Bedford and Hagerman *op. cit.*). Before 1974, less than 150 persons held permits for swordfish fishing with harpoons in California waters (Fig. 11). In 1974, the number more than doubled to about 400.

Fierce competition and conflicts among the harpoon fishermen resulted from the fact that the fishing area is limited to a small region south of Santa Barbara to the Mexican border and within 92 km (50 nmi) of the coast (Fig. 12). To reduce the conflict, beginning in 1976, restrictions were placed on the use of aircraft for

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[1] Available data on dressed length of swordfish average about 1.5 m (5 ft) annually in 1984 to 1988 (D. Bedford pers. comm.).

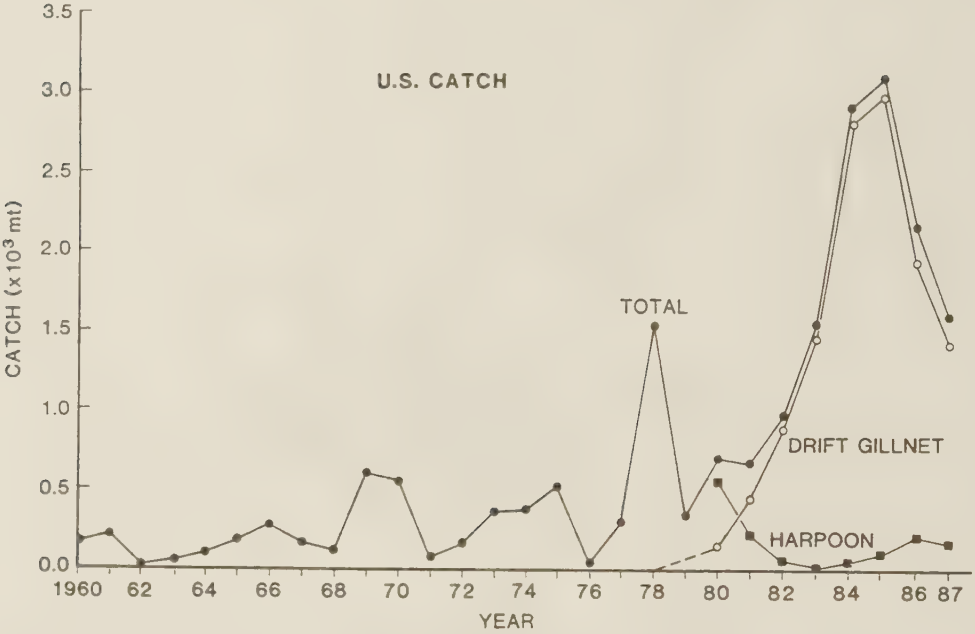

Figure 16. Catch of swordfish by gear for the U.S. fisheries, 1960-1987.

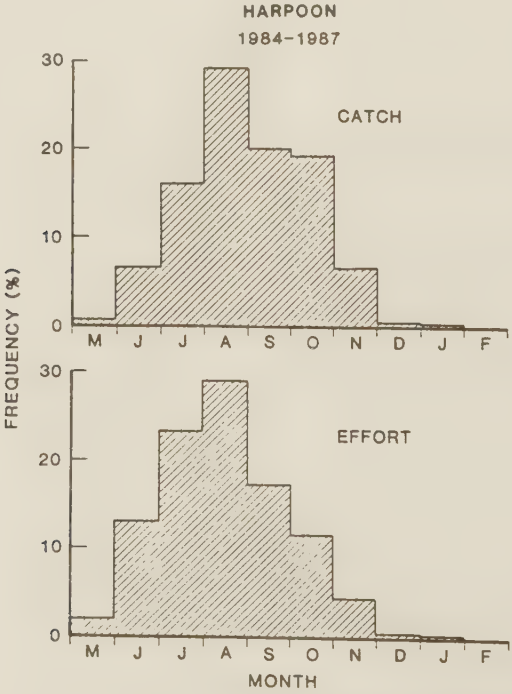

Figure 17. Seasonal distribution of swordfish catch and fishing effort in the U.S. harpoon fishery. (Source: D. Bedford pers. comm.)

assisting swordfish fishermen (Bedford and Hagerman *op. cit.)*. Despite the restrictions, the number of participants continued to grow, peaking at 1,200 permits in 1979 before declining (Fig. 11). Currently, only about 225 permits are outstanding in this fishery.

This reduction in the number of participants can be attributed largely to keen competition from the drift gillnet fishery. The drift gillnet fishery, largely of full-time fishermen, operates in the same fishing area and competes with the harpoon fishery. In the 1970s, when there was no drift gillnet fishery, most of the harpoon permit holders were part-time fishermen, attracted to the fishery that required modest investment. For example, in 1974-1978, only 52% of the harpoon permit holders actually fished for swordfish, about 34% caught swordfish, and 12% landed 50% of the total harpoon catch (Bedford and Hagerman *op. cit.)*. Currently, only the more serious and skilled fishermen remain in the harpoon fishery.

Vessels engaged in swordfish harpooning are mostly between 6 and 15 m (20 and 49 ft) long (Weber ms). Each is equipped with a crow's nest and a "plank" that extends 6 to 9 m (20 to 30 ft) from the bow (Bedford and Hagerman *op. cit.)*. The harpooner stands at the tip of the plank in a "pulpit" and throws the harpoon by hand at the target.

The harpoon consists of a pole of tubular steel construction with an attachment at one end for holding a removable brass or bronze arrow-shaped dart of about 10 cm (4 in.). Holes in the shank of the dart allow attachment of the main line of nylon rope. About 91 m (300 ft) of main line are used, with several neoprene floats or solid PVC balls and a marker-flag attached at the end.

When a fish is harpooned, the main line, floats, and marker-flag are thrown overboard. The fish is allowed to tire from dragging the line, floats, and marker flag, while the vessel pursues other targets. After about 2 to 3 hours, the vessel returns to retrieve the line and fish (Weber ms). The catch is dressed — gutted, head removed back of the cleithrum, and fins trimmed — and stored on ice at sea. Similar dressing of the catch at sea is done by the drift gillnet fishermen.

The catch of the harpoon fishery was at a high point of 600 mt in 1969 and 1970 just before the mercury scare (Fig. 16). The catch collapsed to less than 100 mt in 1971. Recovery followed as demand and prices increased. The catch built back up to 500 mt by 1975. Restrictions on the use of airplanes in 1976 — first as a total ban but, by the end of the year, relaxed to searching outside of 8 km (5 mi) radius of the fishing vessel — disrupted the fishery and the catch fell to only 50 mt. The catch improved the following year as the fishery adjusted to the airplane restrictions. It continued upward, reaching a record of 1,500 mt in 1978. From this peak, it declined sharply to 30 mt in 1983 as the drift gillnet fishery developed and recovered to 160 mt in 1987. Recovery was aided in 1985 by lifting of the restriction on use of aircraft for directing harpoon vessels to swordfish.

Trends and Outlook

The trend of swordfish catches from the Pacific Ocean in recent years is upward (Fig. 4.). Projecting this trend to the future is risky without considering several factors, namely the global market for swordfish, the condition of the stocks, and developments in the longline fisheries.

The world market for swordfish is strong, so prices should remain high. If the market grows at a modest rate of say 5% over 3 years, it will require approximately 1,000 mt of additional swordfish per year, above the 56,000 mt caught worldwide in 1986, to meet the demand.

The Pacific Ocean stocks are in sufficiently good condition (Bartoo and Coan *op. cit.)* to contribute to such an increase. Other major stocks, such as those in the Atlantic Ocean and Mediterranean Sea, are not as healthy. They are showing signs of overfishing, with large numbers of small fish making up the catch (ICCAT *op. cit.)*. These stocks, therefore are not likely to contribute substantially to future increased world supply. In fact, total yield from them could decrease in the long run if stock conditions worsen and the fleets remove smaller fish. Such a decrease will exert pressure on the Pacific fisheries to make up the shortfall.

Except for some coastal fisheries, such as the U.S. fisheries, the Pacific fisheries generally do not target swordfish. Most of these fisheries target tunas and take swordfish as a by-catch; consequently, the markets for tuna will dictate how these fisheries operate and the level of by-catch. The U.S. fisheries target swordfish, and production and catch per unit of effort are declining owing largely to the limited area for suitable operation of the gears and fishing restrictions.

The outlook for coastal fisheries for swordfish is not good, judging from experiences with similar coastal fisheries in the Atlantic Ocean (Caddy 1976). Production is likely to decrease or stall at current levels unless the fisheries expand and exploit additional segments of the stock outside the traditional fishing areas. This will be difficult to do because the fishable areas where the gears are most effective are limited.

In contrast, the longline fisheries of the Pacific have the greatest potential for improved catches of swordfish. Longline fishing effort currently targets the more abundant tunas for the high-value markets, particularly the Japanese sashimi market. This Japanese sashimi market is limited and undergoing strains because of oversupply and instability of prices (Yamashita ms). Discussions among the major suppliers, i.e., Japan, Korea, and Taiwan, are being held to bring stability to the market. If successful, longline fishing effort on tunas could be cut back and the excess effort directed towards other species such as swordfish. Targeting longline effort to swordfish can be easily done by night fishing in certain areas.

As for the outlook of U.S. production of Pacific swordfish, the trend is downward or leveling off. Production is severely limited because the current gears, drift gillnets and harpoon, are effective only in a limited coastal area. Although current state laws allow for experimental gear permits, the restrictions on them and on use of alternative gears, including longlines, and on incidental catches, discourage innovation in catching and landing swordfish (Squire ms). Lacking modification of these restrictions, there is little incentive for investment in new ways to expand the fisheries and increase U.S. production of swordfish from the Pacific Ocean.

Summary

Swordfish are caught in significant amounts only by commercial fishermen. In the Pacific, the catch peaked at 24,300 mt in 1961. The discovery in 1970 of high levels of mercury in swordfish steaks resulted in reduced consumer demand and the catch declining to 11,000 mt in 1971. This decline was short lived, however, as demand returned and production increased to 21,000 mt in 1986.

Approximately 70% of the Pacific swordfish catch is taken with longline gear that is directed at catching tunas, while 30% is taken by surface fishing gears, such as harpoon, drift gillnets, and handlines, directed at catching large pelagic species. Hence, there is little directed fishing for swordfish except for the U.S. fisheries. Both drift gillnets and harpoons are used in the U.S. fisheries off southern California to target swordfish. The total catch for these fisheries was 2,600 mt in 1986 and 1,600 mt in 1987. About 96% of this catch is made by the drift gillnet fishery.

The outlook for the Pacific fisheries is mixed. The world market for swordfish is strong, so prices should remain high. Greater yields appear to be available from the Pacific swordfish stocks as they are in good condition. Increased production by coastal fisheries operating in traditional areas, however, appears unlikely owing to limitations of the gears and suitable fishing areas. In contrast, longline fisheries have considerable potential for increased catches of swordfish. The current fisheries are largely day-fishing operations and directed at catching tunas. They can be redirected to night-fishing operations in certain regions to target swordfish.

For the U.S., the outlook is not good. Pacific swordfish production is severely limited because the gears used are effective only in a limited coastal area. Furthermore, government restrictions on use of alternative gears and on incidental catches discourage efforts to expand the fisheries and increase production.

Acknowledgments

The tasks of assembling data and information on such a large subject as the swordfish fisheries of the Pacific would not have been possible without cooperation from my colleagues. Special acknowledgement is due Atilio Coan, Norman Bartoo, James Squire, and David Holts of the Southwest Fisheries Center (SWFC) for assistance and ideas. My colleagues, Yoh Watanabe of Japan, Hsi-Chiang Liu of Taiwan, Talbot Murray of New Zealand, and Dennis Bedford of the California Fish and Game Department provided data used in this report. Witek Klawe of the Inter-American Tropical Tuna Commission and Sam Herrick of the SWFC provided constructive comments on earlier drafts of this manuscript.

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8964

Subtidal Response of the Scotian Shelf Bottom Pressure Field to Meteorological Forcing

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ABSTRACT *Data collected during the Canadian Atlantic Storms Program (CASP) show subtidal variations in subsurface pressure (SSP) to be highly coherent throughout the Scotian Shelf region, and well correlated to fluctuations in the alongshelf component of wind stress (τ^y). Analysis using a frequency-dependent multiple regression model verified that τ^y is the primary source of local forcing to the SSP field, although non-locally generated variations in SSP are also important. The two components of local wind stress and a non-local SSP term combine to explain over 90% of SSP variance on the Scotian Shelf.*

Statistical results describing the response to τ^y change dramatically depending upon the inclusion of non-local forcing. In a model including both types of forcing, the SSP response to local forcing behaves like the solution to a dynamical model forced by time-dependent wind stress with sea-level prescribed to zero at the eastern cross-shelf boundary. Local τ^y forcing becomes more effective to the west and onshore, whereas the phase suggests propagation to the west. The importance of τ^y is reduced at higher frequencies. Describing SSP with a statistical model containing local forcing alone may lead to an incorrect interpretation of SSP dynamics, particularly in the synoptic band where the wind variance is greatest.

Energy originating from a non-local source is most obvious at $\omega > 0.5$ cpd and at locations on the eastern half of the shelf, but plays an important role at all sites and at all frequencies. These variations propagate to the west at speeds of 6.5 ($\omega < 0.2$ cpd), 25–33 ($0.2 \text{ cpd} < \omega < 0.5$ cpd), and 12–17m s^{-1} ($\omega > 0.5$ cpd). The exponential decay scales at all frequencies are ~900 km in the direction of phase propagation. The non-local response is consistent with theoretical estimates of first- and second-mode shelf waves for this region and represents the most direct evidence of shelf wave activity on the Scotian Shelf to date.

RÉSUMÉ *Des données récoltées durant le Programme canadien d'étude des tempêtes dans l'Atlantique (PCETA) montrent que les variations infra-tidales de la pression de fond (PF) sont fortement cohérentes dans toute la région du plateau Scotian, et présentent une bonne corrélation avec les fluctuations de la composante de la tension du vent (τ^y) parallèle au plateau. L'analyse par un modèle à régression multiple, dépendant de la fréquence, a vérifié que τ^y est la source primaire de forçage local du champ de la PF, bien que des variations d'origine non locale de la PF soient également importantes. Les deux composantes (tension du vent locale et terme non local de la PF) combinées, rendent compte de plus de 90% de la variance de la PF sur le plateau Scotian.*

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Les résultats statistiques décrivant la réaction à τ^y *changent dramatiquement si l'on introduit un forçage non local. Dans un modèle incluant les deux types de forçages, la réaction de la PF au forçage local se comporte comme la solution d'un modèle dynamique forcé par une tension du vent dépendante du temps, et où le niveau de la mer est prescrit à zéro à la limite orientale perpendiculaire au plateau. Le forçage local de* τ^y *devient plus effectif vers l'ouest et vers le rivage, alors que la phase suggère des propagations vers l'ouest. Aux fréquences plus élevées, l'importance de* τ^y *est réduite. La description de la PF par un modèle statistique n'incluant que le forçage local, peut mener à une interprétation incorrecte de la dynamique de la PF, particulièrement dans la bande synoptique, où la variance du vent est la plus élevée.*

L'énergie originaire d'une source non locale est évidente surtout à $\omega > 0{,}5$ *cpj et à des stations de la moitié est du plateau, mais elle joue un rôle important à tous les sites et à toutes les fréquences. Ces variations se propagent vers l'ouest à des vitesses de 6,5 (*$\omega < 0{,}2$ *cpj), 25–33 (*$0{,}2 < \omega < 0{,}5$ *cpj), et 12–17m* s^{-1} *(*$\omega > 0{,}5$ *cpj). Les échelles de décroissance exponentielle à toutes les fréquences sont d'environ 900 km le long de la direction de propagation de la phase. La réaction non locale est en accord avec les estimations théoriques des premières et secondes harmoniques des ondes de plateau pour cette région, et représente l'évidence la plus directe, obtenue jusqu'à présent, de l'activité des ondes de plateau sur le plateau Scotian.*

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1 Introduction

Meteorological forcing has been shown to be an important source of energy to Scotian Shelf dynamics at 2–10 d periods (Petrie and Smith, 1977; Smith et al., 1978; Sandstrom, 1980). Because of its intensity, the typical Canadian East Coast winter cyclone can produce sizable fluctuations in sea-level and current. The complete sea-level or current signal is often a complex summation of modes combining energy from local wind forcing and non-locally generated free waves. Spatial irregularities in the wind regime and bottom topography, and the presence of density stratification can further complicate the response. To account for these uncertainties requires simultaneous measurements of sea-level, current, and atmospheric parameters resolved on sufficiently small spatial and temporal scales. CASP provided such an opportunity on the Scotian Shelf. To complement a uniquely concentrated set of meteorological observations, a suite of oceanographic instruments was deployed to measure variations in sea-level, current, water mass properties, and the wave field on two scales: synoptic – O(1000 km) – and mesoscale – O(100 km).

Results from this shelf experiment can be used to address several fundamental questions pertaining to shelf circulation on these scales. The most basic question concerns the nature of the oceanic response to time-dependent meteorological forcing. Although meteorological variations have been shown to be correlated with fluctuations in sea-level and current, the frequency-dependence of this relationship and its dynamical implications are not clearly understood. In addition, the majority of observations previously made on the Scotian Shelf have been restricted to the outer shelf and shelf break regions (Smith et al., 1978; Smith and Petrie, 1982; Petrie, 1983) or have dealt strictly with coastal sea-level (CSL) measurements (Sandstrom, 1980; Thompson, 1986). Because the dynamics of shelf regions near the coast are more sensitive to changes in depth, the concentration of CASP instruments on the inner third of the Scotian Shelf provides new insight into wind-driven motions not readily discernible from coastal or shelf break observations alone.

Another potentially important energy source to the shelf arises from non-local forcing, often seen in the form of coastal trapped waves (CTWs). Petrie and Smith (1977) give indirect evidence for this, but Sandstrom's (1980) results suggest CSL responds as a purely forced wave, driven by the eastward motion of storms. No direct evidence of CTWs has yet been found on the Scotian Shelf. The complete coverage of the CASP bottom pressure and current array provides an excellent and heretofore unavailable source of information for detecting CTWs, if they exist.

The initial analysis of subtidal CASP data concentrates on the response of the subsurface pressure (SSP) field to meteorological forcing. I begin with SSP because it is simple, relatively easy to measure with good precision, and describes the integrated response of the water column. In addition, the SSP signal is a useful diagnostic of local wind forcing as well as CTW modes.

Results are summarized in time series and spectral forms, and a multiple regression analysis is used to describe the frequency-dependent SSP response to local and non-local meteorological forcing. The relative contribution of each component of forcing is discussed as a function of frequency and position on the shelf, and related to simple dynamical theories that may be applicable to the Scotian Shelf.

2 Observations

a *Methods*

The data described and analysed in this paper were obtained during the CASP field experiment. Instruments were deployed on the Scotian Shelf for a period from November 1985 to April 1986 to measure oceanic responses on mesoscale and synoptic meteorological forcing scales (Fig. 1).

An array of bottom pressure gauges deployed along the length of the Nova Scotia coast, supplemented by Canadian Hydrographic Service permanent tide-gauges, monitored synoptic-scale variations of order 1000 km. From west to east, the temporary gauges were located at West Head, Riverport, Sambro, Ship Harbour, Whitehead Harbour and Louisbourg. Permanent sites included Yarmouth, Halifax, North Sydney and Port aux Basques, Newfoundland.

An offshore mooring array consisted of two cross-shelf lines near Halifax (S1–S5) and Liscomb (S9–S11), and a series of moorings along the 100-m isobath (S2, S6–S8, S10). The array was designed to detect mesoscale variations in the current and pressure fields on scales of order 100 km. Bottom-mounted pressure gauges were deployed at stations S1–S10. Pressure gauges were Aanderaa WLR-5 Water Level Recorders with a range of 0–400 psi* and an accuracy of 0.04 psi. With the exception of S3, data return was of high quality.

Tide-gauge data were isostatically adjusted with local atmospheric pressure at each site to be compatible with bottom pressure records. All bottom pressure and adjusted sea-level will be referred to as subsurface pressure (SSP) throughout this paper. The series were low-pass filtered with a 129-weight Cartwright filter (0.036 cph (28 h) half-power cut-off) to remove tidal and inertial energy and were resampled at six-hourly intervals.

Wind (τ) and atmospheric pressure (p^a) data from the Sable Island AES station

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*1 psi ≡ 6.89 kPa.

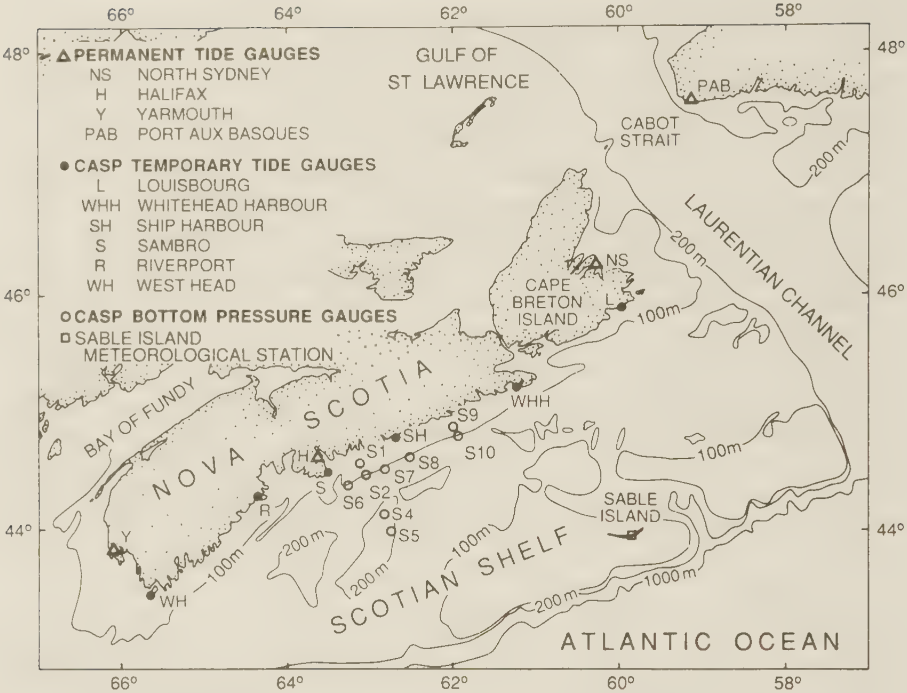

Fig. 1 Map showing positions of bottom pressure (circles) and permanent tide-gauge (triangles) stations, and the meteorological station at Sable Island (square).

(Fig. 1) were chosen to represent meteorological conditions over the Scotian Shelf (Petrie and Smith, 1977). Alongshelf ($+\tau^y = 68°$T) and cross-shelf ($+\tau^x = 158°$T) wind stress components were estimated from wind speed and direction, using the quadratic stress law with a variable drag coefficient (Smith and Banke, 1975). The wind stress and pressure series were filtered and resampled in the same manner as the SSP series. Additional information on the processing of CASP data is given by Lively (1987).

Autospectral variance for all series was calculated according to Carter and Ferrie (1979). The 32 frequency bands each had a bandwidth of 0.0625 cpd. Spectral results were averaged over $n = 14$ blocks of data with 50% overlap, giving $\nu = 22.9$ effective degrees of freedom (Garrett and Toulany, 1982).

b *Time Series*

Low-passed time series plots comparing SSP at stations along the coast and the Halifax line exhibit a high degree of correlation over the entire pressure field (Fig. 2). SSP is also visually quite coherent with alongshelf wind stress. Stress to the east (west) generated a set-down (set-up) of sea-level over the entire shelf, consistent with a cross-shelf surface Ekman flux. These wind-driven events, which occurred in association with the passage of winter atmospheric cyclones, were periodic at about

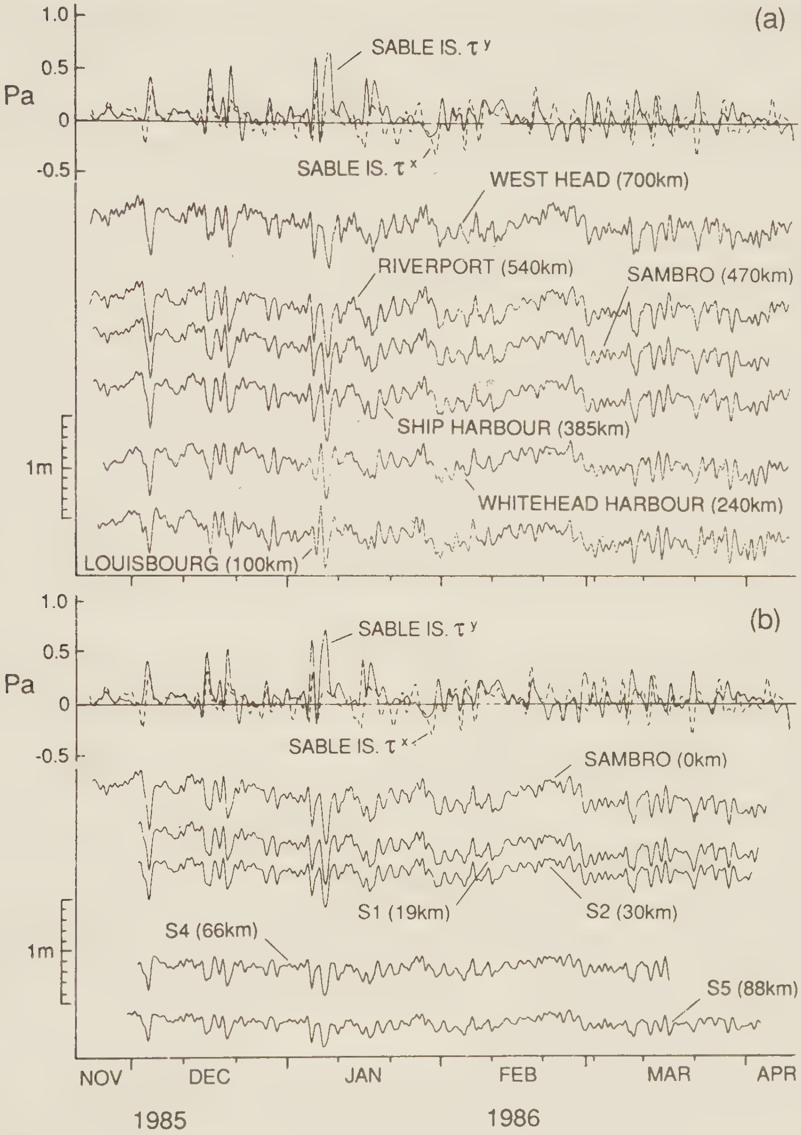

Fig. 2. Time series of Sable Island cross-shelf (τ^x) and alongshelf (τ^y) wind stress components, and bottom pressure from (a) coastal and (b) Halifax line (S1–S5) gauges. Series have been low-pass filtered and resampled at 6-h intervals. Distance relative to the (a) Laurentian Channel or (b) coast as shown.

2 d with an amplitude of 15–30 cm at the coast. However, the response can be much larger, as evidenced by a 60-cm coastal set-down during a one-Pa easterly stress on 7 January. A very low frequency trend is also discernible throughout the records.

Although not apparent at the scale shown, an east-to-west phase propagation was detected in coastal SSP as well, opposite that of the typical storm track. A similar pattern appeared in the 100-m isobath series. No consistent change in amplitude was evident in the coastal SSP records, although the standard deviations of the series, which vary from 9 to 12 cm, generally increased to the west.

SSP also displayed a large cross-shelf coherence scale. The amplitude of SSP decreased by a factor of about two from the coast to S5, approximately 90 km offshore. Note that the cross-shelf slope (i.e. the difference between S1 and S5) decreased over time, presumably owing to a decreased outflow from the Gulf of St Lawrence (Drinkwater et al., 1979). A slight onshore phase propagation is seen in the Halifax line, although it is approximately an order of magnitude smaller than that of the alongshelf direction.

c *Autospectral Variance*

Both Sable Island wind stress components exhibited a similar frequency distribution of variance, as shown by their spectra plotted in variance-preserving form (Fig. 3a). A majority of variance (50–65%) was concentrated in the 0.2–0.5 cpd band, although a significant amount (20–30%) occurred at lower frequencies ($\omega \leq 0.125$ cpd). The alongshelf stress component (τ^y) was more energetic at all frequencies except 0.313 cpd. Sable Island atmospheric pressure (p^a) showed a similar variance distribution, although this autospectrum contained relatively less energy at $\omega > 0.3$ cpd.

SSP spectra generally reflected a variance distribution similar to the meteorological signals. As expected from the visually correlated time series (Fig. 2), the spectra exhibited a similar distribution of variance at most coastal locations (Fig. 3b). Approximately 50% of the subtidal variance occurred in the 0.2–0.5 cpd band, with a large decrease in variance at $\omega > 0.438$ cpd coinciding with the τ^y spectrum. Again considerable energy (~ 40%) was contained at $\omega \leq 0.125$ cpd.

Coastal SSP generally increased in variance from east to west, most notably at $\omega <$ 0.5 cpd. An exception to this occurred at stations adjacent to the Cabot Strait, where SSP variance at 0.563 cpd was noticeably greater at North Sydney (not shown) and Louisbourg (Fig. 3b). This signal was even stronger at Port aux Basques, on the Newfoundland side of the Strait. It also appears that energy at this frequency does not propagate effectively as shown on the spectral distribution at Whitehead Harbour, only 140 km west of Louisbourg.

SSP variance decreased uniformly with distance offshore in all frequency bands (Fig. 3c). The variance dropped by a factor of two to three over a distance of ~ 100 km, consistent with the time series. The importance of the 0.2–0.5 cpd band was again seen at all locations, but the relative contribution at the lowest frequencies was reduced at the offshore stations (30 vs 40%). Overall, however, the SSP spectra, like the time series, were similar over the entire Scotian Shelf region in the along- and cross-shelf directions. The close agreement with the distribution of variance in the meteorological spectra suggests that local meteorological forcing is an important source for subtidal SSP oscillations.

3 Dynamical model

The total SSP signal at any location on the Scotian Shelf can be expressed as

$$\eta(x, y, t) = \eta^L(x, y, t) + \eta^{NL}(x, y, t). \tag{3.1}$$

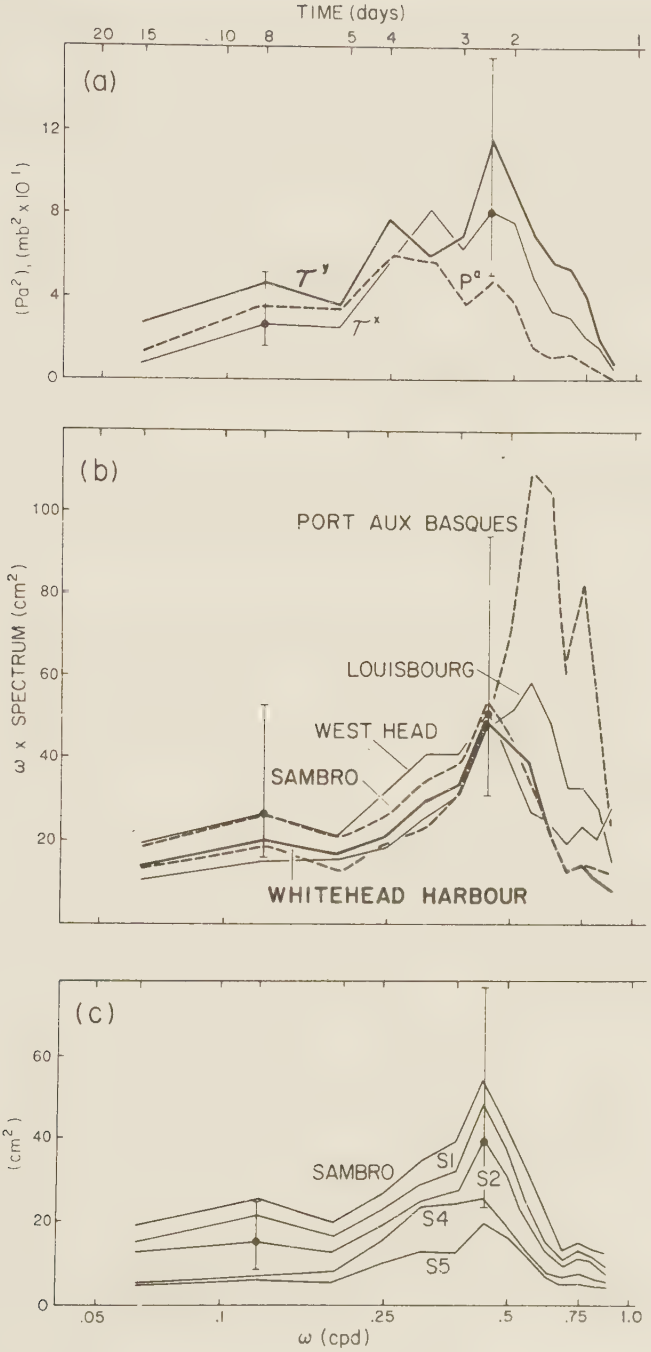

Fig. 3 Autospectra (variance preserved) of low-pass filtered time series for (a) Sable Island wind stress and atmospheric pressure, (b) coastal bottom pressure and (c) bottom pressure from the Halifax line. Representative 95% confidence intervals are shown.

The term η^L defines the locally-forced influence, i.e. the response of SSP to wind stress over the Scotian Shelf. That portion of η whose origin lies beyond the Scotian Shelf is defined by η^{NL}, the free contribution to SSP. These two terms are not necessarily statistically independent, since non-locally forced (free) waves may be generated by a wind stress coherent with that over the Scotian Shelf. These two effects can, however, be separated through a combination of statistical and dynamical arguments.

Initially consider η^L, the expected response of SSP to local wind stress, based on a dynamical shelf model. Assume a long, straight coastline with a right-handed coordinate system such that $x = 0$ at the coast and increases in the offshore direction. Forcing is by a time-varying alongshelf kinematic wind stress $\tau = \tau_0 e^{i\omega t}$. The dynamical model is based on the following homogeneous, linearized, shallow water momentum and continuity equations:

$$-fv = -g\eta_x \tag{3.2}$$

$$v_t + fu = -g\eta_y + \frac{\tau}{h} - \frac{rv}{h} \tag{3.3}$$

$$(uh)_x + (vh)_y = 0 \tag{3.4}$$

where u and v are depth-averaged current velocities in the x (cross-shelf) and y (alongshelf) directions, respectively; η is the local, wind-forced contribution to sea surface elevation (η^L in (3.1)); f is the (constant) Coriolis acceleration; g is the acceleration due to gravity; and r is the linear bottom friction coefficient. Subscripts denote partial differentiation. Harmonic time-dependence of the form $e^{i\omega t}$ is assumed for all time derivatives.

Equation (3.2) has been simplified to a geostrophic balance by taking $\omega/f \ll 1$ and assuming the long-wave approximation $\ell L \ll 1$, where ℓ is the horizontal length scale of the forcing and L is the shelf width. The rigid lid approximation ($\eta_t = 0$) is also made in (3.4). Substituting (3.2) and (3.3) into (3.4) provides a governing equation expressed solely in terms of η;

$$\left(\epsilon h\eta_x - \frac{\tau}{g}\right)_x + h_x\eta_y - h_y\eta_x = 0, \tag{3.5}$$

where

$$\epsilon = \left(i\frac{\omega}{f} + \frac{r}{hf}\right)$$

Eqn. (3.5) is identical to the equation Wright (1986) used to examine the quasi-steady limits of coastal-trapped circulation.

For simplicity, assume an idealized topography that is uniform alongshelf; i.e. $h = h(x)$, and a spatially uniform wind stress; i.e. $\tau = \tau(t)$, at least over a scale ℓ^{-1} much greater than L. These assumptions reduce (3.5) to

$$(\epsilon h\eta_x)_x + h_x\eta_y = 0, \tag{3.6}$$

a parabolic partial differential equation analogous to the heat diffusion equation with

$y < 0$ (i.e. downshelf, in the direction of propagation for free CTWs) replacing the time axis. Thus a disturbance at some point in the field diffuses in the x-direction for increasingly negative y. The steady-state limit of (3.6) is the arrested topographic wave (Csanady, 1978). Other limits and applications of (3.6) are detailed in Wright (1986).

To apply (3.6) to the Scotian Shelf, the bottom topography is treated as a simple-wedge-step shelf profile;

$$h \begin{cases} = h_1\left(\frac{x}{L_1}\right) & 0 < x < L_1 \\ = h_1 & L_1 < x < L \\ = \infty & x > L \end{cases} \tag{3.7}$$

For the Scotian Shelf the wedge and step regions are approximately equal in width ($L \approx 2L_1$). The CASP mooring array was concentrated in the region $0 < x < L_1$, where the most dynamically interesting responses should take place. Within the wedge region $h = sx$, where s is the slope ($= h_1/L_1$), and (3.5) can be expressed as

$$(\epsilon x \eta_x)_x + \eta_y = 0 \qquad 0 < x < L_1. \tag{3.8}$$

In the step region of the shelf $s = 0$, and the solution of (3.6) is trivial.

The boundary conditions are

$$\eta_x(y) = \frac{\tau f}{gr} \qquad x = 0 \tag{3.9}$$

$$\eta(y) = 0 \qquad x = L \tag{3.10}$$

$$\eta_x(y) = \frac{\eta}{L_1 - L} \qquad x = L_1 \tag{3.11}$$

$$\eta(x) = 0 \qquad y = 0. \tag{3.12}$$

Equation (3.9) is obtained because the constraint of no mass flux through the coast requires $v(0, y) = \tau / r$, a balance between surface stress and bottom friction, as $h \rightarrow 0$ (from (3.3)). To keep the geostrophic transport across the shelf break finite requires $\eta_y = 0$ at $x = L$. Since $\eta = 0$ at $y = 0$, it follows that (3.10) must be valid. Because $\epsilon h \eta_{xx} = 0$ for $L_1 < x < L$, η is a linear function of x over the uniform depth region. Since η *and* η_x must be continuous over the change in topography at $x = L_1$ (so that uh is continuous), (3.11) is obtained by evaluating η just inshore of L_1 and differentiating.

Equation (3.12), hence (3.10), presumes η set to zero at some cross-shelf boundary $y = 0$. For the Scotian Shelf, we prescribe $\eta = 0$ at Louisbourg, near the Laurentian Channel (Fig. 1), an appropriate condition if little wind-forced variation in SSP traverses this deep channel. This is a critical boundary condition, since it assumes the Louisbourg SSP signal is associated solely with motions generated remote from the Scotian Shelf. Thus non-locally generated CTWs will be excluded from the solution to (3.6). As Wright et al. (1986) have previously pointed out, the steady response is

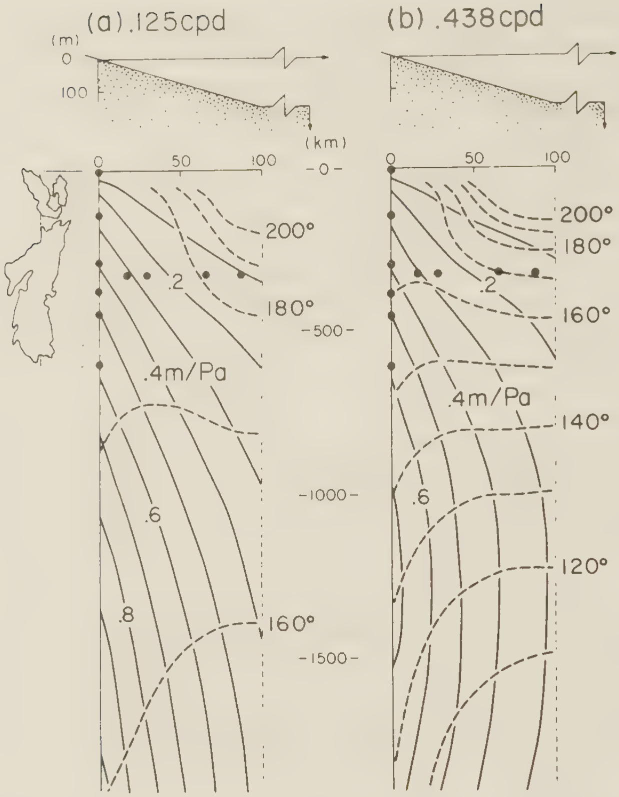

Fig. 4 Solution to Eq. (3.5) for (a) 0.125 cpd and (b) 0.438 cpd for $r = 10^{-3}$ m s^{-1}, $L_1 = 100$ km, $L = 200$ km and $h_1 = 150$ m, and the offshore topography shown. Solid lines define the amplitude (m Pa^{-1}); broken lines define the phase by which η leads τ. Approximate positions of the pressure gauges within the model domain are noted.

highly sensitive to changes in the cross-shelf condition. Thus solutions to (3.6) subject to (3.12) represent only that portion of SSP forced by *local* wind stress (i.e. directly over the model domain), and may be unsatisfactory in describing the *entire* SSP signal on the Scotian Shelf, depending on the magnitude of η^{NL} in (3.1). For simplicity any variation in SSP attributed to wind stress over the shelf region will be defined as the "local" response, while the signal at Louisbourg will be defined as the "non-local" contribution. An alternative to (3.12) could be $\eta = \eta^0$, where η^0 describes the form of the SSP signal observed at $y = 0$; (e.g. a series of CTW modes).

The amplitude and phase of η over the wedge region of the shelf are presented for two different frequencies of alongshelf wind stress forcing; 0.125 cpd (Fig. 4a) and 0.438 cpd (Fig. 4b). These results were obtained by solving (3.6) numerically using boundary conditions (3.9–3.12), and assuming typical values of $r = 10^{-3}$ m s^{-1}, $L_1 = 100$ km, $L = 200$ km and $h_1 = 150$ m. The distance between Louisbourg and West Head is about $3L$. Amplitude is expressed in units of m Pa^{-1}. Positive phase indicates η leads τ. The approximate positions of the SSP sites whose time series are presented in Fig. 2 are marked for reference.

Several important circulation features are apparent in Fig. 4. The amplitude of the response increases in the direction of free wave propagation and decreases offshore, similar to the steady response found by Csanady (1978). Phase decreases to the west, indicating a propagation of sea-level in the direction consistent with free waves. Friction becomes less dominant at higher frequencies, and alongshelf phase speed increases while the cross-shelf slope decreases. At some distance downshelf, terms that vary in y become small and the cross-shelf mass flux $uh \rightarrow 0$, from (3.4) and the requirement $u = 0$ at the coast. Alongshelf velocity becomes steady, proportional to τ, and decreases with increasing ω. From (3.2) and (3.3) sea-level at any position sufficiently far downshelf is

$$\eta(x) = \frac{\tau f}{gr} \int_x^L \left(1 + \frac{i\omega h}{r}\right)^{-1} dx \tag{3.13}$$

a constant along any isobath. Physically the amplitude is limited by temporal variations in the forcing and the subsequent phase interference of free waves generated at different locations along the shelf.

4 Statistical models

To describe the response of the SSP field to wind stress forcing, a hierarchy of multiple linear regression models in the frequency domain was implemented (Jenkins and Watts, 1968; p. 493). The three models compared here are

$$S(\omega) = \alpha_1 T^y(\omega) + \beta_1 T^x(\omega) \qquad\qquad + \epsilon_1(\omega) \tag{4.1}$$

$$S(\omega) = \alpha_2 T^y(\omega) + \beta_2 T^x(\omega) + \gamma_2 S^{NL}(\omega) + \epsilon_2(\omega) \tag{4.2}$$

$$S(\omega) = \qquad\qquad\qquad\qquad \gamma_3 S^{NL}(\omega) + \epsilon_3(\omega). \tag{4.3}$$

The variables S, T^y, T^x and S^{NL} in (4.1–4.3) define Fourier transforms of the variables SSP, τ^y, τ^x and SSP^{NL}, respectively, where SSP^{NL} (approximated by Louisbourg SSP) is a representation of the non-locally forced contribution to SSP. The coefficients α_i, β_i and γ_i are complex transfer functions and ϵ_i is the residual error associated with each model. Least-squares estimates of α_i, β_i and γ_i give the amplitude and phase of the SSP response to each individual forcing term as well as the multiple coherence squared (R_i^2) due to the model for each frequency band. Garrett and Toulany (1982) provide further details of this technique. A comparison can be drawn between this method and that applied by Freeland et al. (1986) in the time domain.

To aid in the interpretation of the statistical analyses, results are described for specific key frequencies representing three bands of interest in the low-passed spectra. Variability at frequencies below the dominant wind band ($\omega < 0.2$ cpd) is represented by 0.125 cpd. The peak of maximum variance in the majority of SSP spectra (0.438 cpd) represents fluctuations in the synoptic band (0.2–0.5 cpd). Results at 0.625 cpd describe the response in the band between maximum wind and tidal forcing (0.5–1.0 cpd). The models (4.1–4.3) will be referred to as models L, L + NL, and NL, respectively, where L implies local and NL non-local forcing effects are included.

a *Local Forcing*

Recall that the "local" forced response refers to that portion of SSP due to a (presumed) homogeneous wind stress over the Scotian Shelf, represented by Sable Island stress. Although wind forcing near the eastern boundary of the shelf undoubtedly generates motions that propagate freely to the west, such motions are considered part of the locally forced response in the statistical models.

With a few minor exceptions, the alongshelf wind stress component τ^y was the dominant wind-forcing term in models L and L + NL (4.1–4.2), with the cross-shelf component τ^x of only secondary importance. Atmospheric pressure p^a was generally an unimportant contributor to SSP when added to L. Further, the SSP response to p^a and, to a lesser extent, τ^x was not statistically significant once τ^y effects were considered. It is therefore believed that τ^y is the principal source of energy to the SSP field via local meteorological forcing, in agreement with the forcing prescribed in the dynamical model of Section 3. Description of the statistical models transfer functions will be limited to τ^y. Results from models L and L + NL are summarized in Figs 5–7 in terms of the amplitude and phase of the SSP response at the coastal stations and S1–S5, the cross-shelf line.

The response to τ^y allows Scotian Shelf SSP observations to be related to the time-dependent solution given by the wind-forced dynamical model in the previous section. The transfer function at 0.125 cpd in both statistical models (Fig. 5) featured a pattern similar to that of the dynamical model. From east to west, the modulus or amplitude $|\alpha_i|$ of the gain increased while the phase ϕ_i decreased slightly, opposite that of a typical low-pressure system that deepens and intensifies as it moves eastward through the region. Both ϕ_i and $|\alpha_i|$ decreased in the offshore direction. The addition of p^a into model L had no effect on SSP response to τ^y, but the additional term SSP^{NL} in L + NL acted to substantially reduce $|\alpha_2|$ and bring ϕ_2 closer to 180° at all sites, relative to $|\alpha_1|$ and ϕ_1. For a 1-Pa alongshelf wind stress to the west, sea-level at the coast rose by 30–70 cm (e.g. 62 cm at Sambro) according to model L, but only 0–50 cm (42 cm at Sambro) by L + NL.

At 0.438 cpd an even greater difference in statistical model results was seen (Fig. 6). $|\alpha_1|$ was larger relative to lower frequencies, but little systematic change in $|\alpha_1|$ was apparent along the coast. In contrast, $|\alpha_2|$ exhibited a pattern similar to that seen at 0.125 cpd. In particular note how $|\alpha_2|$ extrapolates to zero near the Cabot Strait, while $|\alpha_1|$ values are much greater at the upshelf boundary. This is apparent at higher frequencies as well. The difference between $|\alpha_1|$ and $|\alpha_2|$ at 0.438 cpd was also greater than that at 0.125 cpd at all sites. Alongshelf ϕ_1 and ϕ_2 variations imply a similar westward motion. At all sites ϕ_i was farther from 180° than observed at lower frequencies, presumably owing to the decreased importance of friction as seen in the dynamical model.

The SSP response to τ^y at 0.125 and 0.438 cpd as determined from models L and L + NL are also compared with the dynamical model solutions in Figs. 5 and 6. This relatively simple model, with idealized topography and alongshelf homogeneity, does a reasonable job of estimating the amplitude of the wind-forced response and describing the patterns of this response for the Scotian Shelf.

Finally, consider the response to τ^y at frequencies higher than those of the synoptic band; e.g. 0.625 cpd (Fig. 7). The alongshelf and cross-shelf pattern of $|\alpha_i|$ was

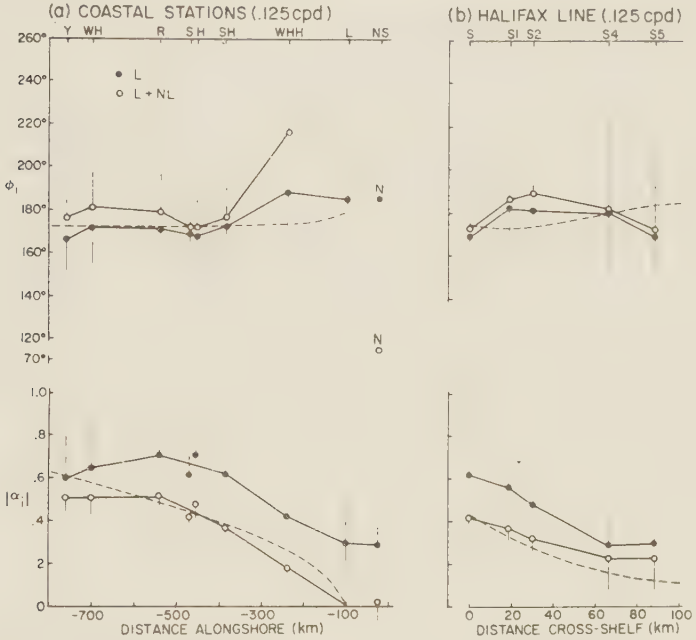

Fig. 5 Phase ϕ_i and amplitude $|\alpha_i|$ of SSP response to Sable Island alongshelf wind stress τ^y at 0.125 cpd for (a) coastal stations and (b) the Halifax line. Solid circles represent the response from model L, open circles represent the response from model L + NL. Errors bars represent the 95% confidence limits. The absence of error bars denote sites where $|\alpha_i|$ is not significantly different from zero. SSP leads τ^y by ϕ_i. Broken lines denote dynamical model results, taken from Fig. 4.

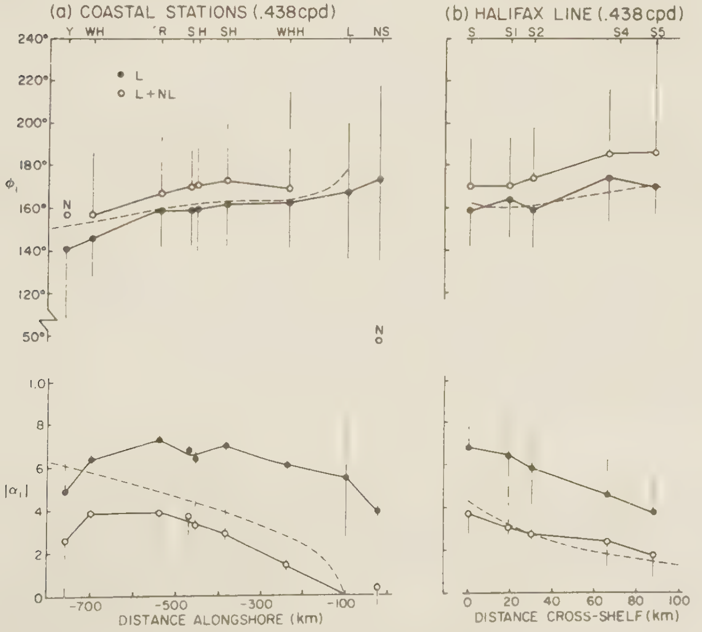

Fig. 6 As for Fig. 5, except for 0.438 cpd.

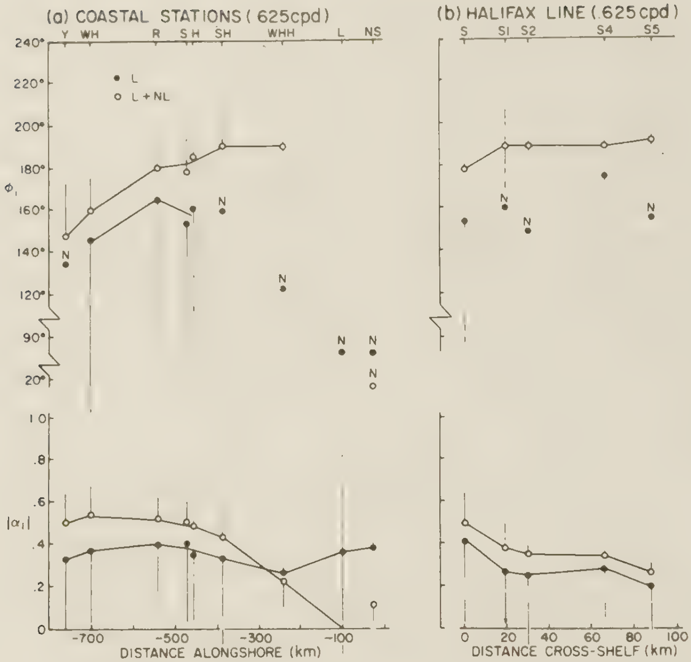

Fig. 7 As for Fig. 5, except for 0.625 cpd.

similar to that seen at 0.438 cpd, although values of $|\alpha_1|$ were much smaller, and of $|\alpha_2|$ larger at the higher frequency. The difference between ϕ_1 and ϕ_2 was also larger; ϕ_2 showed a consistent decrease of ~ 40° along the coast from Whitehead Harbour to Yarmouth, whereas the direction of propagation implied by ϕ_1 was somewhat ambiguous. The cross-shelf ϕ_i exhibited no directional preference.

In summary, alongshelf wind forcing is an important source of energy for SSP oscillations over the inner Scotian Shelf. However, the inclusion of non-local influences in the statistical model substantially reduces the estimated response of SSP attributed to local τ^y alone. This is particularly true in the synoptic band, where $|\alpha_2|$ replicates the pattern of the dynamical model while $|\alpha_1|$ has large amplitudes and no alongshelf trend. The disparity between models L and L + NL demonstrates that statistical results may lead to improper conclusions if not reinforced by some physically relevant theory. Thus it is essential to include non-local forcing to obtain a reasonable representation of the subsurface pressure field.

b *Non–local Forcing*

The additional term in model L + NL contains the complex transfer function γ_2, which accounts for SSP variations after local forcing effects due to wind stress have been removed. Therefore any free wave energy propagating onto the shelf will be accounted for by the non-local forcing term. Louisbourg SSP is defined as the non-locally forced contribution to SSP. Results consistent with the dynamical model indicate the response to Sable Island wind stress at Louisbourg was small at low frequencies, suggesting the SSP signal there contained a significant amount of energy originating from a distant source. The anomalous autospectrum at Louisbourg also indicated this was true at higher frequencies as well. Finally, its location adjacent to the Cabot Strait makes Louisbourg SSP a good diagnostic of energy crossing the Laurentian Channel or propagating out of the Gulf of St Lawrence.

The response to SSP^{NL} in L + NL featured a similar pattern at all frequencies, although the magnitude and degree of change were somewhat frequency-dependent (Figs 8–10). In general, $|\gamma_2|$ decreased to the west and offshore, and the phase direction was to the west. At the lowest frequencies (Fig. 8) $|\gamma_2|$ decreased by factors of two and three over the alongshelf (600 km) and cross-shelf (100 km) length scales of the arrays, respectively. Phase ϕ_2 decreased smoothly along the coast, but the cross-shelf change was less certain. Alongshelf $|\gamma_2|$ changed similarly at 0.438 cpd, but the cross-shelf decrease was markedly reduced (Fig. 9). Alongshelf ϕ_2 was again consistent with free-wave propagation. The general pattern was most obvious at 0.625 cpd (Fig. 10).

As noted above, the transfer functions between SSP and τ^y were sensitive to whether or not the SSP^{NL} term was included in the model. The response to SSP^{NL} also changed with the inclusion of wind forcing in the regression. Model NL defines the correlation between SSP at Louisbourg and other sites. Estimates of SSP coherence scales at each frequency may be made from these results.

It is important to note the substantially different exponential decay scales of SSP, depending upon whether or not local forcing is removed. In contrast with the results from L + NL, $|\gamma_3|$ no decrease from unity away from Louisbourg at 0.125 and 0.438 cpd, but increased alongshelf to values of 1.1–1.2 (Figs 8 and 9). The increase in spectral variance along the coast at $\omega < 0.5$ cpd (Fig. 3) is reflected in this result, implying a coherence scale at least 600 km. At 0.625 cpd, however, $|\gamma_3|$ decreased precipitously downshelf of Louisbourg, suggesting an exponential decay scale of ~300 km (Fig. 10). Again this is consistent with the pattern in the spectral variance. The distribution of ϕ_3 along the coast at all frequencies indicates a westward propagating SSP signal, similar to ϕ_2.

At all frequencies $|\gamma_2|$ and ϕ_2 exhibit an excellent fit as a function of distance y downshelf from Louisbourg. Best fits of the form $\hat{\phi}_2 = a + by$ and $|\hat{\gamma}_2| = ce^{dy}$ were made for each set of values from the coastal stations. The North Sydney response is included for reference.

From b, the slope of the ϕ_2 linear regressions, a phase speed can be determined. Phase speed was westward at all frequencies, consistent with the expected free-wave propagation. The magnitude of the slope varied with frequency. Knowing the slope and associated standard error a phase speed, $c = \omega/b$, was estimated with an appropriate standard error for each frequency.

At 0.125 cpd, $c \approx 6.5$ m s^{-1} with the standard error giving a range of 5–10 m s^{-1}. The phase speed at 0.438 cpd was $c \approx 26$ m s^{-1} (S.E. = 22–33 m s^{-1}), while $c \approx 16$ m s^{-1} (S.E. = 13–20 m s^{-1}) at 0.625 cpd. A dispersion diagram was constructed (Fig. 11), with $k = b/2\pi$, by similarly estimating the phase speed at each frequency band. For comparison, phase-speed estimates for the Kelvin wave ($c = (gH)^{1/2}$), shelf wave for a step shelf ($c = fL$), and first and second mode shelf waves for a wedge shelf ($c_1 = 0.7fL$, $c_2 = 0.13fL$) have been added to the figure. These approximations are based

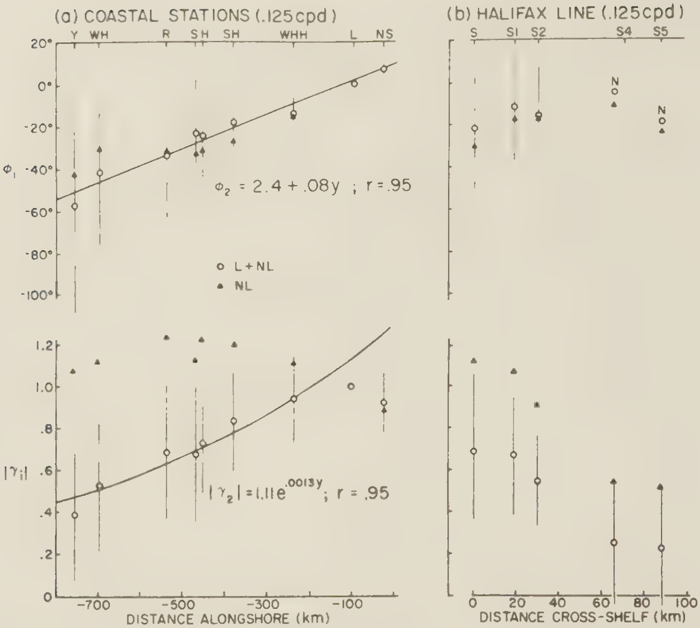

Fig. 8 Phase ϕ_i and amplitude $|\gamma_i|$ of SSP response to SSP^{NL} at 0.125 cpd for (a) coastal stations and (b) the Halifax line. Circles represent the response from model L + NL, and triangles represent the response from model NL. Error bars (95% confidence intervals) are included only for ϕ_2 and $|\gamma_2|$. Bold lines denote the best linear and exponential regression fits to ϕ_2 and $|\gamma_2|$, respectively, as a function of distance y downstream from Louisbourg.

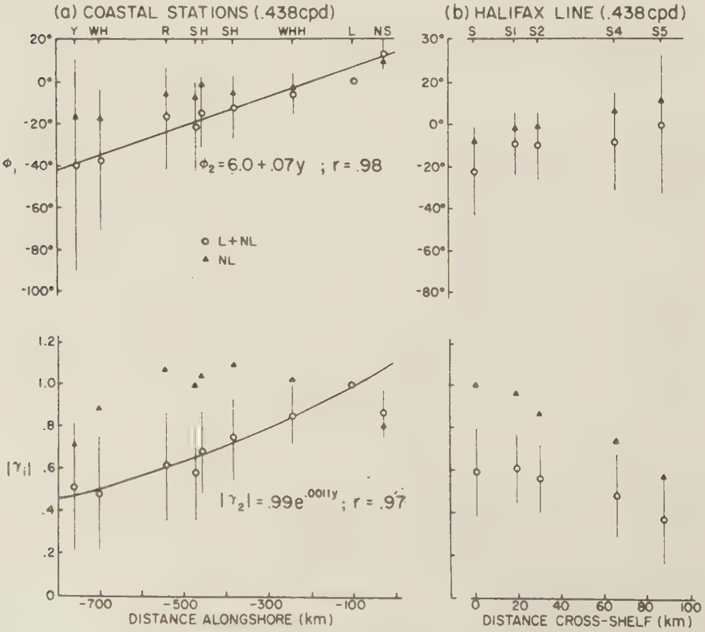

Fig. 9 As for Figure 8, except for 0.438 cpd.

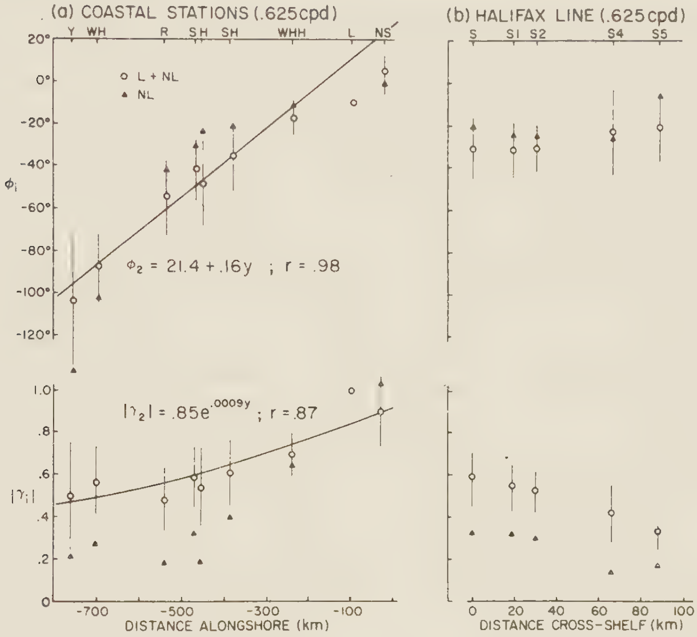

Fig. 10 As for Fig. 8, except for 0.625 cpd.

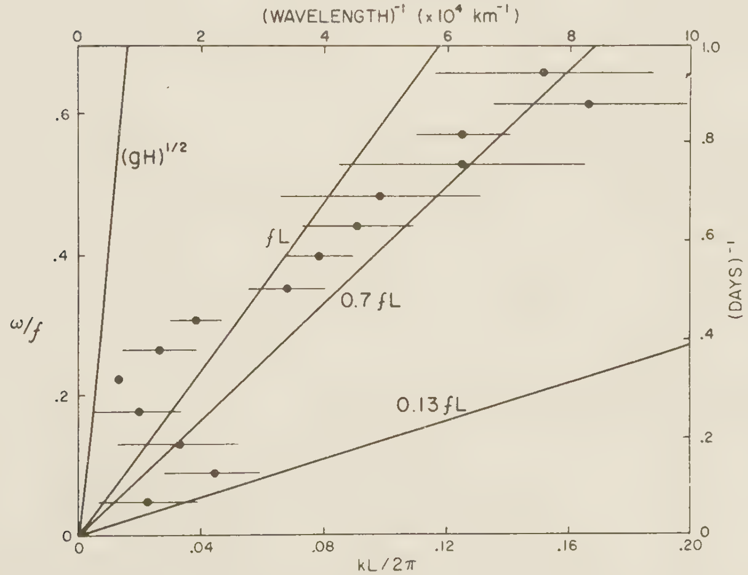

Fig. 11 Dispersion diagram comparing free-wave phase speed for each frequency band with phase speeds for Kelvin wave, step-shelf shelf wave ($c = fL$), and first ($0.7\,fL$) and second ($0.13\,fL$) mode wedge-shelf shelf waves ($H = 2000$ m, $L = 200$ km, $f = 10^{-4}\ \mathrm{s}^{-1}$). The circles represent phase speeds (± standard error) determined from the regression of phase on alongshore distance at each frequency, as shown in Figs 8a–10a.

on coastal trapped wave (CTW) theory from Huthnance (1981) using a deep water depth $H = 2000$ m and shelf width $L = 200$ km.

The three frequency bands examined previously separate themselves according to phase speed. For $\omega > 0.5$ cpd, phase speeds were 12–17 m s^{-1}, falling neatly between the lowest mode shelf wave speeds for the two extremes in shelf profile. However, the propagation was not necessarily uniform along the length of the coast. The phase speed at 0.625 cpd decreased to the west, corresponding to a narrowing shelf. From Louisbourg to Riverport (~ 400 km) the phase lag was ~ 40°, giving $c \approx 26$ m s^{-1}. From Riverport to West Head a similar lag occurred over only 200 km, thus $c \approx 13$ m s^{-1}. Estimating the shelf width as narrowing from 250 to 150 km yields a decrease in free wave speed ($c = fL$) from 25 to 15 m s^{-1}, in close agreement with the observed change in speed. Thus not only do shelf waves appear to propagate along the Scotian Shelf, but phase speeds suggest the waves slow down along the narrowing shelf.

Phase speeds at $\omega < 0.2$ cpd were ~ 6.5 m s^{-1}, about twice the second mode speed. Those in the 0.2–0.5 cpd band were 25–33 m s^{-1}, twice those observed at higher frequencies and greater than the maximum possible lowest CTW mode phase speed. Thus although the high-frequency phase speed was directly interpretable as a single mode wave, propagations at lower frequencies suggested a more complex model structure. These discrepancies are not too surprising, since numerous other studies of CTW motions have found that the observed phase speeds can be as much as 2–4 times greater than those predicted by theory (cf. Schwing et al., 1988). The non-local portion of the response found by Freeland et al. (1986), determined with a method very similar to the multiple regression technique applied here, also demonstrated that free motions propagate at speeds about 25% greater than theory would suggest.

The amplitude of the SSP response to non-local forcing also decreased uniformly to the west with an exponential decay scale of ~900 km at all frequencies. The alongshelf decay scales of first and second mode frictional shelf waves should be approximately 1200 and 200 km, respectively, for the appropriate Scotian Shelf parameters. The lowest mode estimate agrees reasonably with the observations, although the scale for the second mode is smaller than those seen. A more detailed analysis is required to determine the modal structure of the free response. However, the character of the non-local response strongly suggests that CTW activity is important, and is the most direct evidence of shelf waves on the Scotian Shelf to date.

c *Comparison of Local and Non-local Forcing*

Figure 12 summarizes the multiple coherence squared (R^2) attributed to the three statistical models. The triangles represent the amount of variance in each coastal SSP signal explained by model NL. R_3^2 decreased away from Louisbourg at all frequencies. A comparison of R_3^2 values at 0.125 and 0.438 cpd (Figs 12a and b) with those at 0.625 cpd (Fig. 12c), which drop to zero only 300 km downshelf, suggests that SSP coherence length scales were smallest at frequencies where the stress was weak. Little change in cross-shelf R_i^2 occurs at $\omega > 0.125$ cpd for all three models.

Consider now model L, which describes the variance due to local wind stress

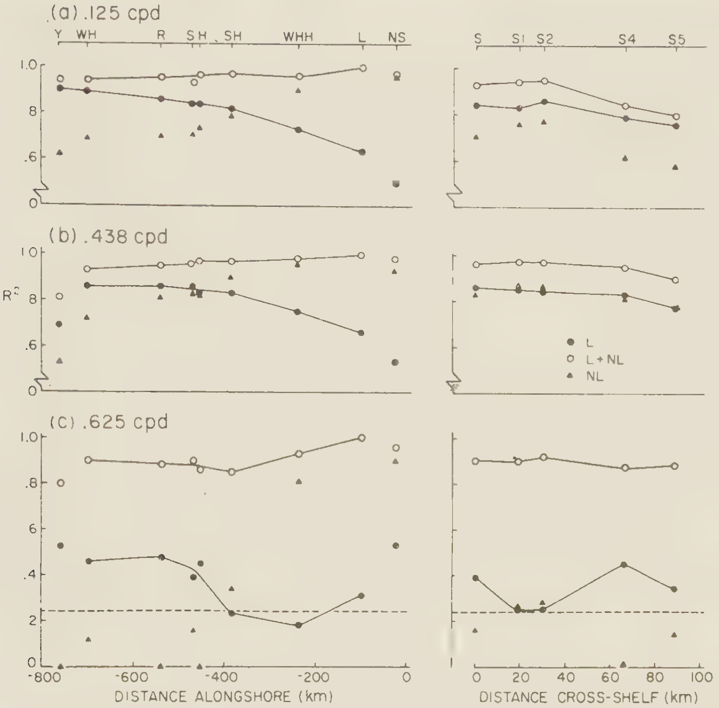

Fig. 12 Multiple coherence squared (R^2) attributed to models (4.1)–(4.3). Solid circles represent R_1^2, open circles represent R_2^2 and triangles represent R_3^2 at (a) 0.125, (b) 0.438 and (c) 0.625 cpd. The 95% level of significance is 0.24.

forcing only (solid circles in Fig. 12). The model was most effective at frequencies having high stress variance. R_1^2 increased to the west at all frequencies, in contrast to R_3^2. This tendency was particularly evident at $\omega < 0.5$ cpd, which implies that SSP responded more coherently to local forcing at frequencies where the dynamical model is valid.

Finally, consider the variance explained by the model L + NL containing local and non-local effects (open circles in Fig. 12). R_2^2 values for this model were consistently high ($R_2^2 \geq 0.9$), decreasing only slightly at higher frequencies or with distance downstream. Cross-shelf values of R_2^2 also show the increased effectiveness of L + NL. The difference between the values represented by the open and solid circles (the solid lines in Fig. 12) demonstrates how much more effective L + NL was, compared with a model considering local wind stress effects alone.

This comparison dramatically demonstrates the importance of free-wave energy in the SSP field, especially east of Halifax and at higher frequencies where the wind energy was low. Non-local effects were particularly evident at 0.625 cpd, where R^2 values doubled and even tripled with the addition of SSP^{NL} as a variable.

The contrast with the poor correlation of model NL is striking. Coastal SSP correlation scales were small at higher frequencies, suggesting the total SSP signal

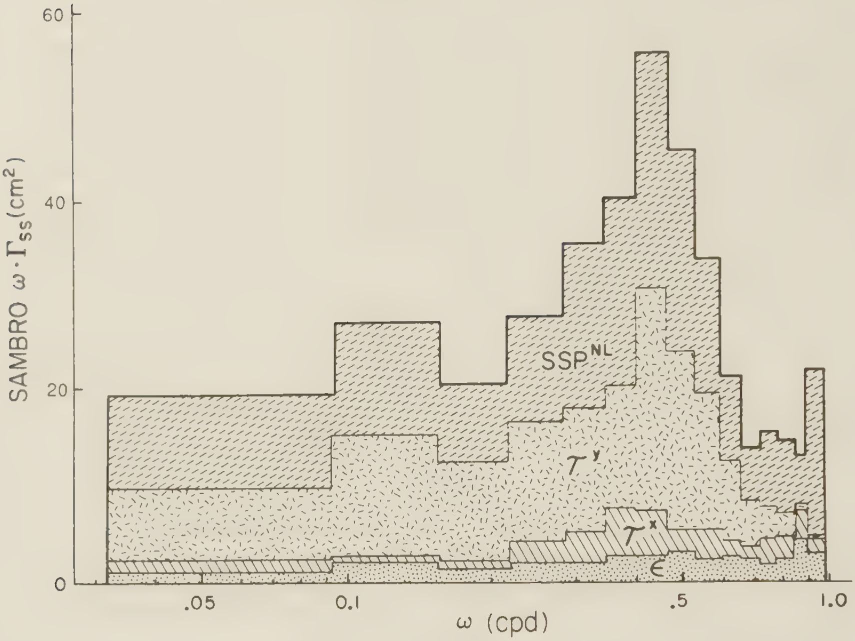

Fig. 13 Distribution of variance in Sambro SSP due to τ^y, τ^x and SSP^{NL} in model L + NL. Each level of shading represents the amount of variance due to each independent variable. The stipled area at the bottom denotes ϵ for the complete model.

was modified by local wind effects while the energy propagated downshelf. However, the residual SSP signal (i.e. after removal of wind effects) at all shelf positions was well correlated with the original free-wave signal at the eastern boundary of the Scotian Shelf, indicating that free energy travelled relatively unperturbed down the shelf. Local wind influences produced an evolution of, but did not necessarily dominate, the SSP field.

Figure 13 summarizes the frequency-dependent contributions of the three terms in L + NL at a representative SSP station (Sambro). The SSP variance in each frequency band is displayed in histogram form. Each region of shading represents the amount of variance attributed to each of the three independent variables. The figure demonstrates the nearly equal importance of local wind stress and non-local forcing at low frequencies ($\omega < 0.5$ cpd). The secondary role of τ^x is also seen. Finally note the increased importance of non-local forcing at higher frequencies ($\omega > 0.5$ cpd). Error in the complete model L + NL, represented by the stipled area under the histogram, is less than 10% of the total SSP variance. These results are generally applicable at all SSP locations, with non-local effects becoming more important at sites nearer the Laurentian Channel and slightly less important downstream of Sambro. However, it is important to note that the variance explained by the three terms described here remained essentially the same at all stations.

5 Discussion

Subtidal SSP variations during CASP are obviously dominated by two influences: local alongshelf wind stress and free-wave energy of a non-local, but possibly meteorological origin. How do these results compare with previous observations on the Scotian Shelf and on adjacent shelf regions? The results described here confirm other data suggesting the Scotian Shelf response is largely wind-driven (cf. Petrie and Smith, 1977; Smith et al., 1978; Sandstrom, 1980), but are incompatible with Sandstrom's data (1980) regarding free waves. An analysis of Sandstrom's data using a model with forced and free-wave contributions may produce different results.

These results are consistent with observations to the north and south as well. Observations from regions upstream of the Scotian Shelf are rather limited but SSP records from the central Labrador Shelf exhibit a distribution of variance with frequency similar to that shown here, and feature southward phase speeds highly suggestive of CTWs (J.F. Middleton, pers. comm.). Recent work by Wright et al. (1987) has provided a reasonable theory relating much of the Labrador Shelf SSP variability to atmospheric pressure-generated CTWs originating from Hudson Bay at 2–6 d periods. Thus free-wave energy from a very distant source apparently can propagate along the Labrador Shelf. The close visual agreement between the spectral responses of SSP off Labrador and Nova Scotia implies that free energy of a similar form, reinforced by local wind stress, can travel large distances and may reach the Scotian Shelf.

Subtidal wind and SSP energy west of the Scotian Shelf is concentrated at periods greater than 2.7 d, and SSP is highly coherent spatially and forced by meteorological transients (Beardsley et al., 1977). Cross-shelf variations in SSP variance on Nantucket Shoals, and the response to alongshelf stress (Brown et al., 1985), are very similar to those seen in the Halifax line. Noble and Butman (1979) analysed adjusted CSL and wind stress at several locations north of North Carolina, including Halifax and Eddy Point, N.S., near Whitehead Harbour. Many of their results agree with findings presented here. Sea-level and wind were spatially coherent at scales > 1200 km. The wind-driven response was almost exclusively due to alongshelf stress and increased from Eddy Point to Halifax. The amplitude of the Halifax SSP response to alongshelf stress was estimated to be 1 m Pa^{-1}. This response is similar in magnitude to that calculated in model L, where only local forcing was considered. However, it has been shown here that combining local and non-local terms in a statistical model substantially reduced the τ^y response. The range of 0.3–0.5 m Pa^{-1} found by Thompson (1986) using a regression model that considered local stress and non-local processes is more consistent with the values of $|\alpha_2|$ discussed here. Had Noble and Butman (1979) included some non-local effect in their calculations, a smaller estimate of the SSP response to alongshelf stress might have been obtained.

In a subsequent paper analysing the alongshelf current response in the Georges Bank and Middle Atlantic Bight regions, Noble et al. (1983) found 75–90% of the low-frequency (60–360 h) energy was due to combined wind-driven and free propagations. The transfer coefficient of alongshelf stress to current increased to the southwest, and a form of the arrested topographic wave model (Csanady, 1978) gave good estimates of the observed current response. Phase speed estimates of free waves were similar to those reported here. Although the ratio of free to forced energy decreased in the free direction, the absolute free energy contribution increased in that direction as well, suggesting that CTWs are reinforced by incoherent wind stress fluctuations (i.e. non-linear transient wind responses over Georges Bank). Unfortunately their results were not separated into finer frequency bands.

The low-pass filtered SSP times series from the Labrador and Scotian Shelves exhibit a net phase speed in the free direction. It is much more difficult to discern free-wave propagations in the adjusted signals from the northern Middle Atlantic Bight. Noble and Butman (1979) and Wang (1979) observed southward (free) waves in the region south of Cape May. However, free waves in the north are masked by northward-directed forced waves. The resultant phase speeds north of Cape May suggest a combination of forced and free waves (Noble and Butman, 1979; Wang, 1979). Farther south in the South Atlantic Bight, the data are less uniform, but evidence for both types of forcing has been documented (Brooks, 1979; Schwing et al., 1988).

The combined effects of local alongshelf stress and distantly generated free waves are certainly the primary controlling factors of subtidal SSP along the entire east coast of North America. The relative importance of each factor depends very much on the geographic position, the frequency of the variations considered and even the time of year (Schwing et al., 1988). The similarity of the SSP response on the Scotian Shelf to those in the Labrador Shelf and Middle Atlantic Bight–Georges Bank regions suggests a continuum of meteorologically driven processes, with large-scale topographic effects (e.g. Laurentian Channel, Georges Bank) coming into play. However, small-scale topographic features, like those on the Scotian Shelf, do not appear to be a major impediment to subtidal SSP variability.

These results have at least one other important implication for modelling strategies. In addition to suggesting appropriate model types to explain the physics behind the forced and free responses of the Scotian Shelf, the relationship of the transfer functions provides information to evaluate proper upshelf boundary conditions (i.e. Laurentian Channel) for Scotian Shelf models. The interpretation of these results can also be used to infer upshelf boundary conditions for Gulf of Maine models. Although they are not precisely known, Wright et al. (1986) have shown that proper conditions are necessary to achieve accurate "steady-state" model results.

6 Summary

Subtidal SSP on the inner portion of the Scotian Shelf is controlled by two primary forces – local alongshelf wind stress and non-locally generated free wave energy. Cross-shelf stress is of only minor importance. Together these terms explain more than 90% of all SSP variance. However, the relative importance of these factors depends on geographical position and frequency.

The response of SSP to local forcing exhibits the features of a dynamical model forced by a time-dependent alongshelf wind stress and clamped at the upshelf boundary. SSP is most coherent with τ^y, and the response amplitude increases with distance downshelf. The signal also propagates in the free direction. Cross-shelf coherence and amplitude decrease, and phase propagates offshore.

The free response decreases in coherence and amplitude with distance offshore and away from its upshelf source, much like a classic CTW (Gill and Schumann, 1974). It is observed at all frequencies, but the relative contribution of non-local energy to the SSP signal is greatest at frequencies where the stress is weak. The effectiveness of non-local forcing also is greater at locations nearer Cabot Strait. Phase speeds along the coast are consistent with first and second mode CTWs. These results provide the most direct evidence of CTW on the Scotian Shelf to date, and imply that the Laurentian Channel does not completely block free-wave energy from propagating downstream.

A substantial change in the statistically estimated response to τ^y is observed when the non-local contribution to SSP is ignored. This disparity is greatest at frequencies with the highest wind variance. The response to τ^y in the complete model compares more favourably with that in the dynamical solution. Thus a statistical model considering both local wind stress and free waves of a non-local origin is a more physically reasonable representation of SSP dynamics.

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8965

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ADVANCES IN KNOWLEDGE AND PRIORITIES FOR RESEARCH, TECHNOLOGY AND MANAGEMENT RELATED TO ARTIFICIAL AQUATIC HABITATS

William Seaman, Jr., Raymond M. Buckley and Jeffrey J. Polovina

The reasons for use of artificial structures to create habitat for fishes and invertebrates, and/or enhance fisheries have only strengthened since they were enumerated by Buckley et al. (1985) in an introduction to the proceedings of the Third International Artificial Reef Conference. Evidence of accelerated worldwide interest and effort in this field is provided by comparison of that conference, held in 1983, and the Fourth International Conference on Artificial Habitats for Fisheries, for which this paper provides a program summary and introduction to the technical proceedings. For example, in 1983, 43 presentations and 14 posters described research and technology in seven nations, whereas in 1987, 94 oral reports and 37 posters depicted effort in 19 countries (Seaman, in press).

In this paper we report highlights of research, technology and some management according to the conference sessions in which information was presented and discussed. A more general summary of all 1987 conference events is provided in newsletter format (Seaman and Welch, 1988), and one of the special sessions is reported in a volume of abridged papers (Reggio, in press). Planning, sponsorship and additional comparisons with three previous conferences are described by Seaman (in press).

The overall purpose of the conference was to organize and evaluate research and development intended to enhance aquatic habitat and therefore fishery populations in freshwater and marine ecosystems. Although utilization of artificial aquatic habitats has occurred for centuries, scientific description of their function and impact has been only recent (Bohnsack and Sutherland, 1985). To some degree, inquiry in freshwater and marine systems represents different bodies of knowledge which the conference sought to unify, although most information came from estuarine and oceanic settings.

Overview of Global Efforts

Centers of activity for artificial habitats for fisheries include portions of Australia, Japan, southeastern Asia, the Caribbean and eastern and northern Mediterranean basins, the Pacific Islands, and North America. Much of the effort is focused on coastal marine environments, although lake, reservoir and lotic freshwater systems are also addressed. The papers and abstracts in these proceedings review planning and programs in certain geographic areas, as well as results of research and development in individual nations and at specific sites.

Interest in manmade habitat has gone beyond benthic artificial reefs to include structures deployed at various depths in the water column (i.e, fish aggregating devices, or FADs). Experience with both broad types of habitat has been gained by major user interests, including commercial seafood harvesters, artisanal fisheries, and recreational interests. Environmental management interests, meanwhile, continue recent evaluations of bottom reefs as mitigation for habitat alteration or loss.

Planning at a national level is restricted to at most a few governments. Japan continues to be the most technologically sophisticated in terms of extensive deployment of specifically designed massive structures in pursuit of national goals for commercial seafood production in territorial waters. In contrast, the United States plan provides a framework in which numerous state and local governments and private interests work autonomously, largely in pursuit of private recreational fisheries (and some diving) objectives, with virtually no federal expenditure for deployment.

Seafood harvest is clearly the primary objective of most habitat creation efforts worldwide, in artisanal and more industrial settings. Most commonly, materials are acquired opportunistically from surplus manmade or readily available natural products, such as concrete block or brushpiles, respectively. Only in Japan has a large infrastructure of commercial reef-building interests developed.

Increasingly, artificial reefs and other structures are viewed as fishery management tools for use in concert with other practices. A particular concern is that deployment of reefs and FADs should be accompanied by regulations restricting fishing effort and gear at the structures. Rather than being used in isolation strictly to enhance exploitation of populations aggregated for harvest, artificial habitats may serve conservation purposes. For example, reefs have been deployed in Monaco and Thailand to prevent trawling in certain inshore habitats. Reefs to serve as reproduction or nursery sites are used for a number of species in Japan, and in the United States include lingcod spawning (Washington) and spiny lobster refuge (Florida). Fishing effort in urban areas in Washington has been relocated away from heavily utilized natural reefs, by creating reefs for pier and boat facilities.

Advances and Priorities

Growth of a multidisciplinary database for artificial aquatic habitats has accelerated in the mid-1980's, primarily on a spatial basis as additional investigators have initiated research and technology transfer at new geographic locations. Conversely, long-term study has been conducted at only a limited number of sites. Gradually, descriptive studies are being augmented by more quantitative efforts. Despite various individual studies of benthic reefs during the modern history of fishery science, with increased effort in recent years (Bohnsack and Sutherland, 1985), this field is still relatively new. For example, assessment of both economic impacts as well as certain ecological parameters has been initiated only in about the last decade, and indeed rigorous techniques still are in development. Bohnsack and Sutherland (1985) determined that in multi-year periods in 1966–1983 the average number of peer-reviewed artificial reef publications ranged between 4.4 and 8.0 annually, principally in natural and engineering sciences.

At the Fourth International Conference on Artificial Habitats for Fisheries technical sessions were organized both for subjects of historical interest with a more extensive literature (i.e., ecology, engineering, fishery management, mitigation) and for new areas (i.e., techniques of environmental assessment and monitoring, economics and policy, conversion of obsolete petroleum platforms to permanent fishery habitats, artisanal fisheries). These are summarized below, not as annotated accounts of all presentations, but with reference to trends, major findings, or identified needs:

Ecology.—This session received the most papers (21), reflecting past scientific emphasis. Evidence for in situ biological production of certain artificial reef sites and also for aggregation of organisms from surrounding habitats suggests that questions related to attraction and production cannot be cast in an "either-or" dichotomy. An updated approach would be to consider a continuum along which attraction and production vary in relation to one another in terms of providing a source of animal populations at given locations.

Ecological characterization of benthic reefs has included description of physical conditions, such as currents, and patterns of community succession. Less information is available for FADs. Information needs include how the life history requirements of individual species may be addressed in design features of artificial habitats, especially recruitment and survival of juveniles. Study of trophic dynamics as well as the relative importance of shelter and recruitment limitation is emerging as an area of interest. Continuing needs for long-term research, rigorous experimentation, and utilization of artificial habitats as sites for more classical studies were identified.

Engineering.—Structural design and performance of Japanese reefs reflect the most intensive efforts in this field, which overall is relatively new and significantly less sophisticated worldwide. Limited experimentation and quantification has been conducted at U.S. Atlantic coast sites. Fabrication of specific reef structures is not common, in contrast with continuing widespread.deployment of materials that are acquired opportunistically. There is a need to integrate biological investigations of species requirements with engineering studies of materials design, placement, and performance physically. Limited technology transfer of Japanese habitats has occurred. Joint studies, as well as evaluation of different levels of cost and complexity to achieve similar levels of biological productivity are required.

Fishery Management.—Despite limited scientific explanation of what makes a reef, FAD or other structure effective from a biological standpoint—in terms of defining how a particular physical structure meets ecological requirements of one or more given species—artificial habitats recently have gained widespread acceptance as a tool of fishery science. Moreover, their utilization in many areas, particularly in commercial or recreational fishing situations, has evolved away from an orientation of maximizing exploitation. Uses of artificial habitat in resource conservation are being assessed. Furthermore, questions about the intended goal of manmade habitat need to be answered prior to deployment.

There is some debate over the institutional and organizational arrangements best suited to plan and implement habitat programs. In many areas, private fishing interests secure and deploy materials on the basis of self-interest, whereas close governmental agency management of reef and other programs is the only avenue used for habitat enhancement in other areas.

Mitigation.—The practice of using artificial aquatic habitat to replace a natural habitat that has been impaired by human action only recently has used benthic reefs as a mitigation technique. Worldwide, as reported to the conference, apparently has occurred only on the Pacific coast of the contiguous United States mainland, where both rocky reef habitat and secondarily established macro-vegetation have been created. Management-oriented research in Washington has developed a list of "biota indicators" for use in siting reefs in temperate waters, with good assurance that a given assemblage of organisms will colonize the habitat. Testing of this index methodology in other settings, and long-term assessment of reefs as mitigation techniques, are two subjects recommended for further investigation.

Environmental Assessment and Monitoring.—This facet of reef-related research and technology has received a disproportionately small amount of effort. It has been demonstrated quantitatively that various traditional fish censusing methods, for example, are not directly comparable. Whereas common visual assessment techniques may produce highly correlated rankings of species on reefs of similar size, estimates of actual abundance can vary significantly according to method (e.g., line transect, point census, etc.). Thus different field procedures can cause marked bias in data on fish abundance.

Additional fishery science practices that are in stages of refinement or require new apparatus include optimal size of sample area, and hydroacoustic and video sensing.

Economics and Policy.—Just as development of government policy toward artificial habitats has lagged their actual widespread deployment in the last two decades, so has policy-related research lagged the actual implementation of policy. Ownership and use patterns are variable, including private and common property holdings, and goals for food and recreation purposes. In such an extremely heterogeneous situation no uniform international policies toward reefs, FADs, and related structures have emerged. Japanese managers have declared that reef-based fisheries are operating on a long-term sustainable basis, for example, whereas in artisanal settings shorter term efforts to maximize production have not been evaluated. Impacts of artificial habitat-centered fisheries on other elements of the resource base have not been evaluated extensively. Further clarification of goals is foreseen, as reefs emerge as accepted fishery management tools, and as both their popularity and the opportunity for conflict among users increase. Economic assessment of actual performance of artificial habitats has been limited, so that unambiguous linkage of fishing and catch rates to given species has been difficult. Recent study has determined that design and location features controlled by planners are important to economic performance of artificial habitat. New research should include interdisciplinary approaches by economists, biologists and social scientists.

Artisanal Fisheries.—Artificial reefs and fish aggregating devices are frequently and successfully used to create fishing areas near artisanal villages in several nations. In the Philippines, for example, pyramid shaped artificial reefs are constructed by villagers from locally available bamboo. Current research in the Philippines is using concrete reinforced with bamboo to build reefs with an improved life span. Not only do the artificial reefs provide fishing sites but it is thought that they also help show that reef structure is valuable and hence reduce destructive fishing applied to natural reefs.

In Thailand the government has deployed a number of experimental artificial reefs near artisanal fishing villages. The reefs, made of concrete and tires, provide habitat which attracts the more commercially valuable reef related species compared to the species previously found on the soft bottom habitat. In areas heavily fished by trawlers, the artificial reefs are useful simply if they close an area near the villages to trawlers.

Petroleum Platform Conversion.—The increasing availability of obsolete offshore petroleum production platforms as potential fishery habitats has motivated efforts to demonstrate and apply this technology in areas such as the U.S. Gulf of Mexico, where about 4,000 structures ultimately face removal and planned onshore salvage. Other areas of potential application include California, the Caribbean, North Sea, and southeast Asia. Fishery harvest at in situ (operational) platforms includes recreational catch in Louisiana and Texas and mariculture of mussels and other commercial shellfish species in California. In the U.S., there is concern for delays in consideration and implementation of policies to facilitate utilization of obsolete platforms for fishery enhancement. Meanwhile, technical engineering, economic and some biological knowledge of conversion of platforms to permanent habitat has been developed recently. There is remarkable structural similarity between platforms and certain reef units fabricated in Japan.

At a policy level, progress to allow industry to satisfactorily resolve questions of liability has been made, while domestic defense and international legal concerns remain. Emerging study needs include the impacts and alternatives of redeployment of platforms as related to fisheries benefits and existing ecosystems. (See Reggio, in press.)

General Issues.—A clear need for interaction among disciplines is apparent, wherein the objectives and impacts of artificial habitats for fisheries can be evaluated from a broad perspective that includes different user group concerns. This might ensure that goals for habitat enhancement are well-defined prior to actual deployment, and that attainment of objectives can be evaluated in measurable ways. Just as the role of reefs, FADs and related structures has broadened and gained wider credibility in the field of fishery management, continuing expansion of the types of studies of them is also warranted. For example, in the area of ecology, ongoing research regarding colonization, population size or seasonality might be supplemented by analysis of behavior or food webs.

To complement development of new knowledge of artificial habitats, education and technology transfer at lay public and semi-technical levels are required. The growing popularity of reefs, FADs, etc., worldwide warrants that science be employed in guiding new and appropriate deployment efforts to optimize benefits, and minimize costs and negative impacts. Continuing exchange of information among scientists must be accompanied by incorporation of the best available data in ongoing or planned reef and FAD construction. For example, guidance of placement of materials by U.S. recreational volunteer projects could incorporate study designs that evaluate parameters such as spacing, density and profile, thereby taking advantage of structures that might not be affordable through agency or academic budgets. Continuing effort to translate material (Haga and Vik, 1982) is required. Obviously, subsequent international conferences will draw from and enhance a growing network of interests in this field.

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8966

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FEEDING ECOLOGY OF TWO SUBTROPICAL SEABIRD SPECIES AT FRENCH FRIGATE SHOALS, HAWAII

Michael P. Seki and Craig S. Harrison

ABSTRACT

Regurgitated food samples from black noddy, *Anous minutus*, and red-footed booby, *Sula sula*, were collected and analyzed from French Frigate Shoals, Hawaii. Eighteen families of fishes, three families of cephalopods, and miscellaneous crustaceans were found in 396 black noddy samples. The most common prey were identified as fishes belonging to the families Synodontidae, Mullidae, and Microdesmidae and as the cephalopod family Ommastrephidae. Twenty-two families of fishes, primarily the Exocoetidae, Carangidae, and Mullidae, along with ommastrephid squids were found in the 456 red-footed booby samples. Our results suggest that these two species of seabirds are apex, opportunistic predators. Seasonal analyses reflect the variation of prey availability over the course of a year and lend support to the notion that this variation is a controlling factor in the timing of the species' breeding. The relationship between the trophic ecology of the seabirds and a tropical fishery is discussed.

In recent years, interest involving the trophic relationships among seabirds has grown immensely. Much of the related research has been directed toward topics relevant to the management of commercial fisheries and the impact of such fisheries on seabird populations (Nettleship et al., 1984).

Seabirds are generally apex predators in marine ecosystems and, as such, are potential competitors with commercial fisheries. Overfishing (Furness, 1984; Springer et al., 1986) and natural climatic fluctuations such as an El Niño event (Schaefer, 1970; Idyll, 1973; MacCall, 1984; Gibbs et al., 1987) have historically altered the availability, quantity, or quality of seabird food supplies and, likewise, seabird populations of many world oceans. To make management decisions or simply predict the effect of such changes, it is important to know what effects fishing practices are likely to have on seabird populations and, conversely, whether seabirds do indeed compete with commercial fisheries. Idyll (1973) suggested that fishery-seabird competition is most severe when the target involves identical species in identical size classes. Basic to the examination of seabird-fisheries interactions is that we acquire an understanding of the food requirements of the involved species.

In the northwestern Hawaiian Islands (NWHI), fishery development proposals prompted an investigation into the feeding ecology of the 18 breeding species of seabirds. The results of the study are described in Harrison et al. (1983). Although the phenomenally large sample size of the study eclipsed any prior tropical or subtropical seabird trophic study, it was not without deficiencies. In an attempt to represent all seabird species from each island, sampling was still inadequate for anything other than superficial seasonal analyses. Diamond (1983) pointed out that, because the samples were taken from such a large geographical range, the species sampled cannot be said to constitute a community.

Our study was undertaken in an attempt to limit and control geographical and seasonal variables and to establish a baseline from which future sampling could be used to monitor seabird population trends and food availability.

METHODS

Food samples from black noddy, *Anous minutus*, and red-footed booby, *Sula sula*, were collected at French Frigate Shoals in the NWHI. The study site, located at the midpoint of the Hawaiian

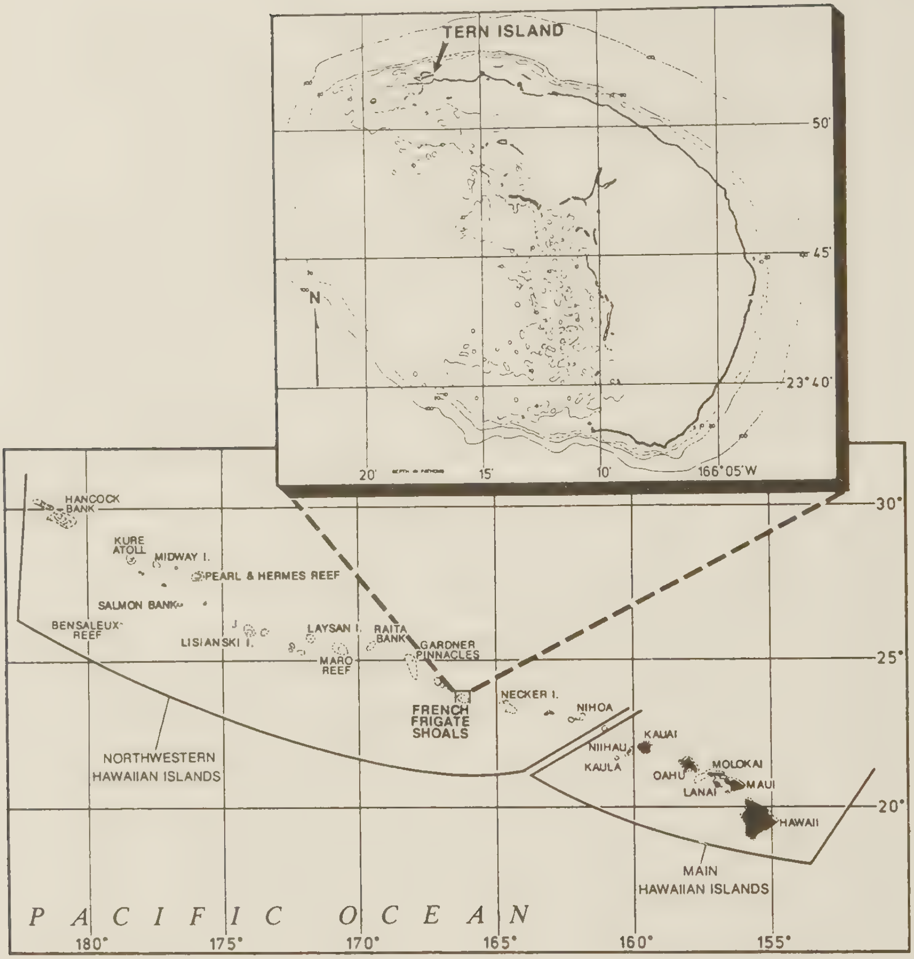

Figure 1. French Frigate Shoals and the Hawaiian Archipelago.

Archipelago at lat. 23°45'N and long. 166°10'W, is a coral atoll consisting of 12 sandy islets and 1 volcanic pinnacle on a platformed crescent-shaped reef. The reef to a depth of 55 m covers about 648 km² and forms a 363 km² lagoon (Fig. 1). Sampling was conducted on Tern Island, the largest of the sandy islets located near the northwest tip of the crescent (Amerson, 1971; Uchida and Uchiyama, 1986).

French Frigate Shoals is influenced during most of the year by the North Pacific high with northeasterly trade winds predominating. Surface water temperatures range from 20° to 25°C during the winter and from 25° to 27.5°C during the summer (Seckel, 1962; Armstrong, 1983).

The decision to study the black noddy and the red-footed booby was based primarily upon their availability to be sampled throughout the year. Five stomach samples from each species were collected weekly between January 1981 and October 1982. Birds were generally captured alive by hand or with a long-handled, polypropylene fish net and induced to regurgitate. Each sample was then preserved in 10% formalin and returned to the laboratory for analysis. Most of the samples were taken from adult birds with sampling efforts concentrated between 1900 and 2300.

Laboratory procedures for examination of the samples were similar to those employed by Harrison et al. (1983). Sample contents were emptied into a fine mesh strainer, rinsed in running water, sorted into identifiable groups, and counted. In lieu of using water displacement to measure prey biomass, food items were blotted dry and wet weights were measured to the nearest 0.1 g. If more than one

Table 1. Number, frequency of occurrence, weight, and index of relative importance (IRI) of the prey items in 396 black noddy food samples at Tern Island, French Frigate Shoals

Prey species	Total no.	% No.	Freq. occur.	% Freq.	Total wt	% Wt	IRI
Crustacea							
Penaeidae	2	0.03	1	0.25	0.5	0.02	0.01
Penaeus marginatus	8	0.13	8	2.02	2.3	0.10	0.46
Brachyura (crab megalopa)	4	0.07	4	1.01	0.4	0.02	0.09
Stomatopoda	13	0.22	3	0.76	0.3	0.01	0.17
Pseudosquilla sp.	1	0.02	1	0.25	0.1	0.00	0.01
Squilla sp.	28	0.47	7	1.77	3.4	0.15	1.10
Lysiosquilla sp.	3	0.05	3	0.76	0.4	0.02	0.05
Cephalopoda							
Teuthoidea	42	0.70	29	7.32	11.0	0.49	8.71
Onychoteuthidae	3	0.05	3	0.76	9.1	0.41	0.35
Ommastrephidae	110	1.83	64	16.16	131.5	5.91	125.08
Sthenoteuthis oualaniensis	16	0.27	11	2.78	62.4	2.80	8.53
Cranchiidae	1	0.02	1	0.25	0.1	0.00	0.01
Cranchia scabra	1	0.02	1	0.25	0.4	0.02	0.01
Osteichthyes (unidentified fishes)	117	1.95	28	7.07	16.7	0.75	19.09
Leptocephali	64	1.07	41	10.35	21.2	0.95	20.91
Clupeidae							
Spratelloides delicatulus	144	2.40	22	5.56	70.2	3.16	30.91
Photichthyidae							
Vinciguerria sp.	13	0.22	1	0.25	6.9	0.31	0.13
Synodontidae	3,294	54.83	271	68.43	861.5	38.73	6,402.31
Trachinocephalus myops	107	1.78	33	8.33	36.7	1.65	28.57
Synodus sp.	23	0.38	7	1.77	3.4	0.15	0.94
Gonorhynchidae							
Gonorhynchus gonorhynchus	29	0.48	17	4.29	23.0	1.03	6.48
Hemiramphidae	1	0.02	1	0.25	0.1	0.00	0.01
Oxyporhamphus micropterus	3	0.05	3	0.76	7.7	0.35	0.30
Exocoetidae	63	1.05	37	9.34	36.7	1.65	25.22
Parexocoetus brachypterus	2	0.03	2	0.51	1.7	0.08	0.06
Exocoetus volitans	5	0.08	5	1.26	5.4	0.24	0.40
Holocentridae	124	2.06	40	10.10	23.6	1.06	31.51
Neoniphon sp.	2	0.03	1	0.25	2.2	0.10	0.03
Neoniphon sammara	1	0.02	1	0.25	2.6	0.12	0.03
Macrorhamphosidae							
Macrorhamphosus sp.	2	0.03	2	0.51	0.6	0.03	0.03
Scorpaenidae	12	0.20	7	1.77	1.1	0.05	0.44
Dactylopteridae							
Dactyloptena orientalis	1	0.02	1	0.25	0.3	0.01	0.01
Echeneidae	2	0.03	2	0.51	0.2	0.01	0.02
Carangidae							
Naucrates ductor	3	0.05	3	0.76	1.4	0.06	0.08
Decapterus sp.	5	0.08	5	1.26	3.1	0.14	0.28
Decapterus tabl	1	0.02	1	0.25	1.8	0.08	0.03
Coryphaenidae							
Coryphaena sp.	3	0.05	3	0.76	1.8	0.08	0.10
Coryphaena equiselis	3	0.05	3	0.76	1.0	0.04	0.07
Mullidae	959	15.96	185	46.72	684.6	30.77	2,183.23
Pomacentridae	1	0.02	1	0.25	0.4	0.02	0.01
Cheilodactylidae							
Cheilodactylus vittatus	2	0.03	2	0.51	1.7	0.08	0.06
Sphyraenidae	5	0.08	4	1.01	1.5	0.07	0.15
Sphyraena sp.	1	0.02	1	0.25	0.4	0.02	0.01
Labridae	6	0.10	5	1.26	1.0	0.04	0.18
Blenniidae	12	0.20	9	2.27	2.9	0.13	0.75

Table 1. Continued

Prey species	Total no.	% No.	Freq. occur.	% Freq.	Total wt	% Wt	IRI
Microdesmidae							
Ptereleotris heteroptera	556	9.25	83	20.96	100.1	4.50	288.20
Gunnelichthys curiosus	2	0.03	2	0.51	0.2	0.01	0.02
Gempylidae	29	0.48	16	4.04	6.3	0.28	3.07
Gempylus serpens	145	2.41	60	15.15	65.4	2.94	81.05
Scombridae	14	0.23	7	1.77	2.1	0.09	0.57
Istiophoridae	2	0.03	2	0.51	0.3	0.01	0.02
Nomeidae	7	0.12	2	0.51	1.3	0.06	0.09
Nomeus gronovii	3	0.05	2	0.51	1.3	0.06	0.06
Pleuronectoidei (flatfishes)	3	0.05	3	0.76	0.6	0.03	0.06
Bothidae	3	0.05	2	0.51	1.1	0.05	0.05
Balistidae	1	0.02	1	0.25	0.2	0.01	0.01
Tetraodontidae							
Lagocephalus lagocephalus	1	0.02	1	0.25	0.4	0.02	0.01

item in the same taxon was present and could not be distinguished as a whole individual, the total weight and number of individuals were recorded. When possible, lengths of the prey were taken, including standard length (SL) for fishes, mantle length (ML) for cephalopods, carapace length for shrimps, carapace width for crabs, and total length for all others. No attempt was made to measure the lengths of any prey items that were well digested.

Prey items were identified to the lowest possible taxon by using the methods described in Harrison et al. (1983). When possible, fishes were identified by external anatomical characters and morphometrics. In many cases, however, the fishes were in an advanced stage of digestion and required clearing of the flesh and staining of the vertebrae with Alizarine S (Taylor, 1967). A combination of vertebral counts and morphological characters was then used for identification. Invertebrates were identified by undigested hard parts and external morphological features. In the case of cephalopods, this included beaks, pens, and luminous organs among other anatomical features; for crustaceans, exoskeletons and walking appendages were the primary identification characters.

To analyze the data, we employed the index of relative importance (IRI) developed by Pinkas et al. (1971) to assess the value of prey items. The IRI incorporates percentage by number (N), weight (W), and frequency of occurrence (F):

$$\text{IRI} = \%F(\%N + \%W).$$

Although this index has its shortcomings (Hyslop, 1980), it provides a basis for ranking the prey items that is representative of the three measures traditionally used in stomach content analyses. Because the objective of the study was to identify the major prey and their importance to the birds, we excluded the unidentifiable remains from the IRI analyses.

To examine effects due to seasonal variation in prey availability as reflected by any differences in diet, the data were separated by season [winter (December–February), spring (March–May), summer (June–August), and fall (September–November)] and then analyzed.

RESULTS

Black Noddy.—Three hundred and ninety six black noddy samples were collected and analyzed for this study. Regurgitated samples averaged 5.7 g and 15.2 prey items (Table 1). Overall, the diet was composed of fishes (IRI = 18,287.5), cephalopods (IRI = 316.1), and crustaceans (IRI = 7.94). The fishes, representing 18 families, occurred in 98.2% of the samples, comprised 90.0% of the total aggregate weight, and accounted for 96.1% of the total number of food items. Fish families with the highest IRI values were Synodontidae (IRI = 6,723.0), Mullidae (IRI = 2,183.2), and Microdesmidae (IRI = 296.15). To a lesser degree, Gempylidae and Holocentridae also were common forage items. Nearly all of the fishes taken as prey were juveniles or larvae; unfortunately, this meant that many of the specimens were not identifiable beyond the family level. The only synodontid that was

Table 2. Percent frequency of occurrence of prey families by season for the black noddy at Tern Island, French Frigate Shoals

Prey families	Winter (N = 98)	Spring (N = 121)	Summer (N = 111)	Fall (N = 66)
Penaeidae	6.12	1.65		1.52
Brachyura (crab megalopa)	2.04			3.03
Stomatopoda	7.14	1.65	3.60	1.52
Teuthoidea	11.22	7.44	6.31	3.03
Onychoteuthidae	1.02	0.83	0.90	
Ommastrephidae	20.41	11.57	18.92	27.27
Cranchiidae	2.04			
Unidentified fishes	10.20	4.96	6.31	7.58
Leptocephali	11.22	11.57	4.50	16.67
Clupeidae	1.02	1.65	15.32	3.03
Photichthyidae		0.83		
Synodontidae	92.86	70.25	42.34	75.76
Gonorhynchidae	13.27	2.48	0.90	
Hemiramphidae		1.65		3.03
Exocoetidae	7.14	6.61	17.12	9.09
Holocentridae	5.10	3.31	9.01	34.85
Macrorhamphosidae	2.04			
Scorpaenidae	3.06	0.83	1.80	1.52
Dactylopteridae				1.52
Echeneidae			1.80	
Carangidae	3.06	3.31	1.80	
Coryphaenidae	1.02	0.83	2.70	1.52
Mullidae	20.41	59.50	61.26	37.88
Pomacentridae	1.02			
Cheilodactylidae		0.83	0.90	
Sphyraenidae	1.02	3.31		
Labridae	4.08			1.52
Blenniidae	4.08	2.48	1.80	
Microdesmidae	44.90	4.96	9.01	37.88
Gempylidae	25.91	19.01	12.61	19.70
Scombridae		2.48	1.80	3.03
Istiophoridae			0.90	1.52
Nomeidae	2.04	1.65		
Pleuronectoidei	2.04	0.83		
Bothidae	2.04			
Balistidae				1.52
Tetraodontidae				1.52

identified to species was *Trachinocephalus myops*, and no mullids were identified beyond family, a problem also encountered during the Harrison et al. (1983) study. *Ptereleotris heteroptera* comprised nearly all of the microdesmids with the exception of two *Gunnelichthys curiosus*. The pelagic ommastrephid squids were the most important cephalopod, and stomatopods were the most important crustacean.

None of the previous studies effectively examined seasonal differences in diet composition. In this study, we found that the prey items that ranked high when all data were pooled remained high when the data were separated by season (Table 2), although the order of their ranking may have changed. With the assumption that the birds are high-level, opportunistic predators, we believe that this result reflects seasonal changes in prey availability. The frequency of occurrence of the highest ranked families was plotted against season and analyzed by years. We extracted the data for black noddies sampled at French Frigate Shoals in 1978–1980 from the Harrison et al. (1983) study for inclusion in this analysis (Fig. 2).

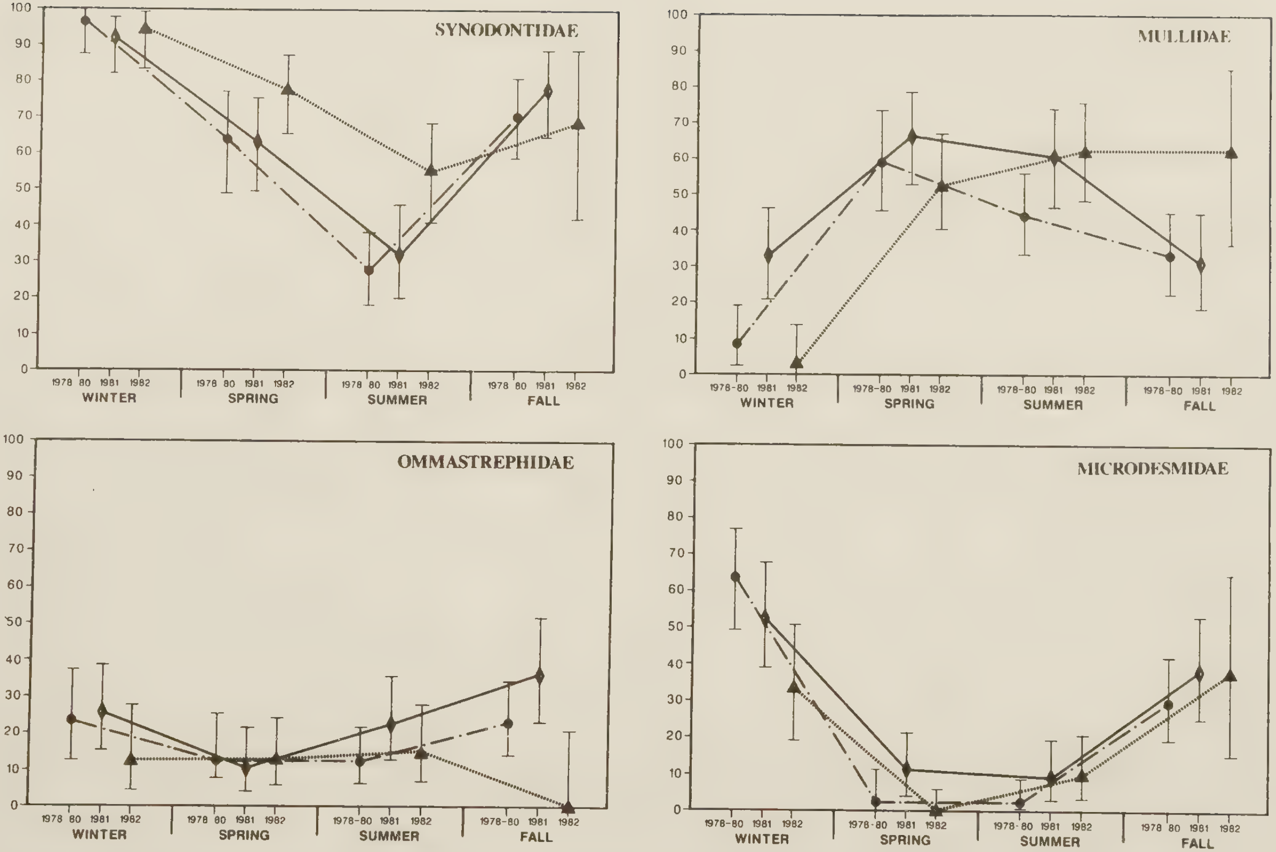

Figure 2. Seasonal frequencies of occurrence and the 95% confidence limits of major black noddy prey families at French Frigate Shoals. The 1978–1980 data are from Harrison et al. (1983).

Table 3. Number, frequency of occurrence, weight (in grams), and index of relative importance (IRI) of the prey items in 456 red-footed booby food samples at Tern Island, French Frigate Shoals

Prey species	Total no.	% No.	Freq. occur.	% Freq.	Total wt	% Wt	IRI
Cephalopoda	1	0.04	1	0.22	0.6	0.00	0.01
Teuthoidea	22	0.91	16	3.51	70.9	0.19	3.86
Ommastrephidae	704	29.10	214	46.93	4,597.9	12.21	1,938.68
Ommastrephes sp.	1	0.04	1	0.22	14.4	0.04	0.02
Ommastrephes bartramii	30	1.24	17	3.73	963.4	2.56	14.17
Sthenoteuthis oualaniensis	124	5.13	66	14.47	2,723.7	7.24	178.99
Osteichthyes (unidentified fishes)	9	0.37	7	1.54	28.3	0.08	0.69
Photichthyidae							
Vinciguerria sp.	1	0.04	1	0.22	0.9	0.00	0.01
Synodontidae	5	0.21	1	0.22	1.3	0.00	0.05
Gonorhynchidae							
Gonorhynchus gonorhynchus	13	0.54	5	1.10	16.0	0.04	0.64
Hemiramphidae	36	1.49	29	6.36	444.0	1.18	16.98
Oxyporhamphus micropterus	41	1.69	30	6.58	992.3	2.64	28.49
Euleptorhamphus viridus	26	1.07	20	4.39	871.6	2.32	14.88
Hyporhamphus acutus pacificus	1	0.04	1	0.22	2.8	0.01	0.01
Exocoetidae	480	19.84	276	60.53	12,181.3	32.36	3,159.67
Parexocoetus brachypterus	145	5.99	77	16.89	3,261.7	8.66	247.44
Exocoetus sp.	65	2.69	48	10.53	3,217.0	8.55	118.36
Exocoetus volitans	24	0.99	16	3.51	1,107.2	2.94	13.79
Exocoetus monocirrhus	2	0.08	2	0.44	143.1	0.38	0.20
Cypselurus sp.	10	0.41	9	1.97	955.1	2.54	5.81
Cheilopogon sp.	6	0.25	6	1.32	545.9	1.45	2.24
Hirundichthys speculiger	2	0.08	2	0.44	176.7	0.47	0.24
Holocentridae	2	0.08	2	0.44	2.3	0.01	0.04
Veliferidae							
Metavelifer multispinosus	3	0.12	3	0.66	17.6	0.05	0.11
Priacanthidae	2	0.08	2	0.44	6.2	0.02	0.04
Priacanthus sp.	27	1.12	7	1.54	209.1	0.56	2.59
Priacanthus alalaua	6	0.25	4	0.88	144.7	0.38	0.55
Carangidae	1	0.04	1	0.22	2.3	0.01	0.01
Naucrates ductor	2	0.08	2	0.44	2.2	0.01	0.04
Decapterus sp.	29	1.20	22	4.82	491.9	1.31	12.10
Decapterus macarellus	6	0.25	6	1.32	730.7	1.94	2.89
Decapterus tabl	18	0.74	9	1.97	268.3	0.71	2.86
Decapterus macrosoma	85	3.51	29	6.36	1,511.8	4.02	47.89
Selar crumenophthalmus	4	0.17	3	0.66	41.6	0.11	0.18
Coryphaenidae							
Coryphaena sp.	8	0.33	7	1.54	57.7	0.15	0.74
Coryphaena hippurus	3	0.12	2	0.44	70.8	0.19	0.14
Coryphaena equiselis	8	0.33	8	1.75	332.0	0.88	2.12
Emmelichthyidae	2	0.08	1	0.22	11.5	0.03	0.02
Mullidae	362	14.96	55	12.06	679.7	1.81	202.25
Kyphosidae							
Kyphosus bigibbus	2	0.08	2	0.44	7.7	0.02	0.04
Cheilodactylidae							
Cheilodactylus vittatus	1	0.04	1	0.22	0.9	0.00	0.01
Ammodytidae	3	0.12	1	0.22	0.6	0.00	0.03
Gempylidae							
Gempylus serpens	54	2.23	30	6.58	183.7	0.49	17.90
Scombridae	1	0.04	1	0.22	0.3	0.00	0.01
Auxis thazard	1	0.04	1	0.22	35.9	0.10	0.03
Katsuwonus pelamis	29	1.20	18	3.95	440.0	1.17	9.36
Thunnus alalunga	1	0.04	1	0.22	12.6	0.03	0.02
Istiophoridae	1	0.04	1	0.22	0.4	0.00	0.01

Table 3. Continued

Prey species	Total no.	% No.	Freq. occur.	% Freq.	Total wt	% Wt	IRI
Nomeidae	1	0.04	1	0.22	4.7	0.01	0.01
Nomeus gronovii	2	0.08	2	0.44	3.7	0.01	0.04
Monacanthidae	1	0.04	1	0.22	1.9	0.01	0.01
Tetraodontidae							
Lagocephalus lagocephalus	1	0.04	1	0.22	20.2	0.05	0.02
Molidae							
Ranzania laevis	5	0.21	3	0.66	36.8	0.10	0.20

Using the 1978–1980 data as the initial baseline, there is little difference in the 1981 data and definite trends in the occurrence of the major species in the diet through the course of a year. Winter and fall peaks of synodontid and microdesmid occurrences coincide with lower occurrence frequencies of mullids. Likewise, spring and summer frequencies of mullids in the diet seem correlated with lower frequencies of synodontids and microdesmids. It is likely that these trends also reflect relative abundance of the fishes in the epipelagic environment during these seasons. Samples taken in 1982, however, appear to deviate from the trends of prior years for some of the prey families. For example, the frequency of mullids in the diet increased in fall 1982 when compared to previous years, and ommastrephid squids were absent in the black noddy diets, whereas in previous years their occurrence peaked in the fall. Conversely, the occurrence of microdesmids showed little variation between any of the years.

We collected 386 prey items in sufficiently good condition to obtain reliable length measurements. These prey items ranged in length from 4 mm (brachyuran crab megalopa) to 74 mm (*Gempylus serpens*) ($\bar{x}$ = 32.45 mm, s = 11.49). The smallest fishes among the diet components were three larval scorpaenids, 9 mm each. Among major prey families, Synodontidae (N = 118) were 21–53 mm SL ($\bar{x}$ = 40.1, s = 4.6), Mullidae (N = 21) were 46–62 mm SL ($\bar{x}$ = 52.8, s = 3.9), Microdesmidae (N = 120) were 18–34 mm SL ($\bar{x}$ = 27.8, s = 2.4), and Ommastrephidae (N = 12) were 22–55 mm ML ($\bar{x}$ = 40.5, s = 8.7).

Individual weights of prey items that were nearly intact were also recorded. The 390 measurements ($\bar{x}$ = 0.5, s = 0.7) ranged from numerous items weighing 0.1 g to an ommastrephid squid, *Sthenoteuthis oualaniensis*, weighing 4.3 g. Both length and weight data collection involved only prey items with minimal digestion, and we did encounter a few cases in which some larger prey items had undergone more significant digestion and accurate measurements could not be obtained. These prey are not included in the above summaries, and any resultant bias should be considered.

Red-footed Booby.—We collected and analyzed 456 red-footed booby samples. Food samples averaged 83.0 g and 5.3 prey items (Table 3). Overall, fishes (IRI = 13,200.2) and cephalopods (IRI = 3,192.7) made up the entire composition of prey items identified in the samples. The fishes, representing 22 families, occurred in 93.4% of the samples, comprised 77.8% of the total aggregate weight, and represented 63.5% of the total number of food items. Fish families with the highest IRI values were Exocoetidae (IRI = 6,306.8), Carangidae (IRI = 207.0), and Mullidae (IRI = 202.2). Of the exocoetids identified to species, *Parexocoetus brachypterus* and *Exocoetus volitans* appear to be the most important. Although

Table 4. Percent frequency of occurrence of prey families by season for the red-footed booby at Tern Island, French Frigate Shoals

Prey families	Winter (N = 104)	Spring (N = 129)	Summer (N = 124)	Fall (N = 99)
Cephalopoda			0.81	
Teuthoidea	11.54	4.65	2.42	1.01
Ommastrephidae	45.19	46.51	66.13	47.47
Unidentified fishes	0.96	0.78	3.23	1.01
Photichthyidae				1.01
Synodontidae	0.96			
Gonorhynchidae	4.81			
Hemiramphidae	31.73	13.95	4.03	16.16
Exocoetidae	65.38	85.27	62.10	73.74
Holocentridae			0.81	1.01
Veliferidae		1.55	0.81	
Priacanthidae			6.45	3.03
Carangidae	10.58	3.88	30.65	13.13
Coryphaenidae	4.81	3.10	3.23	3.03
Emmelichthyidae			0.81	
Mullidae	8.65	10.08	20.97	7.07
Kyphosidae	0.96	0.78		
Cheilodactylidae		0.78		
Ammodytidae		0.78		
Gempylidae	4.81	8.53	10.48	1.01
Scombridae			10.48	7.07
Istiophoridae			0.41	
Nomeidae			2.42	
Monacanthidae		0.78		
Tetraodontidae				1.01
Molidae		1.55	0.81	

many of the flyingfishes could not be identified beyond the family level, it is possible that many of the larger cypselurine flyingfishes were the bulk of the unidentified family members. Fishes of the genus *Decapterus* (especially *D. macrosoma*) comprised nearly all of the carangids, and as mentioned earlier, none of the mullids could be identified more specifically. Other fishes that contributed significantly to the red-footed booby diet included halfbeaks (Hemiramphidae), snake mackerels (Gempylidae), and tunas (Scombridae). The pelagic squid family Ommastrephidae (IRI = 2,978.7) accounted for all of the identified cephalopods, most of which were identified as *S. oualaniensis*.

We again found that the prey families that ranked high when all data were pooled, also ranked high when separated into seasons (Table 4). The frequency of occurrence of these prey families was then plotted against season and analyzed by years (Fig. 3). Unfortunately the red-footed booby samples for French Frigate Shoals in Harrison et al. (1983) were insufficient to compare to our current information. Although there are variations between years (especially between ommastrephids and exocoetids), abundances of mullids, carangids, and ommastrephids appear to peak during the summer, whereas exocoetids peak in the spring and are least abundant in the summer. At Aldabra Atoll, Diamond (1974) reported ommastrephids to be most abundant during the wet season (November–March) and exocoetids, although present throughout the year, to be most abundant during the dry season (April–October).

We obtained 245 measurements of prey items with a mean length of 86.4 mm SL (s = 22.4) and ranging from 11 mm ML (*S. oualaniensis*) to 304 mm SL

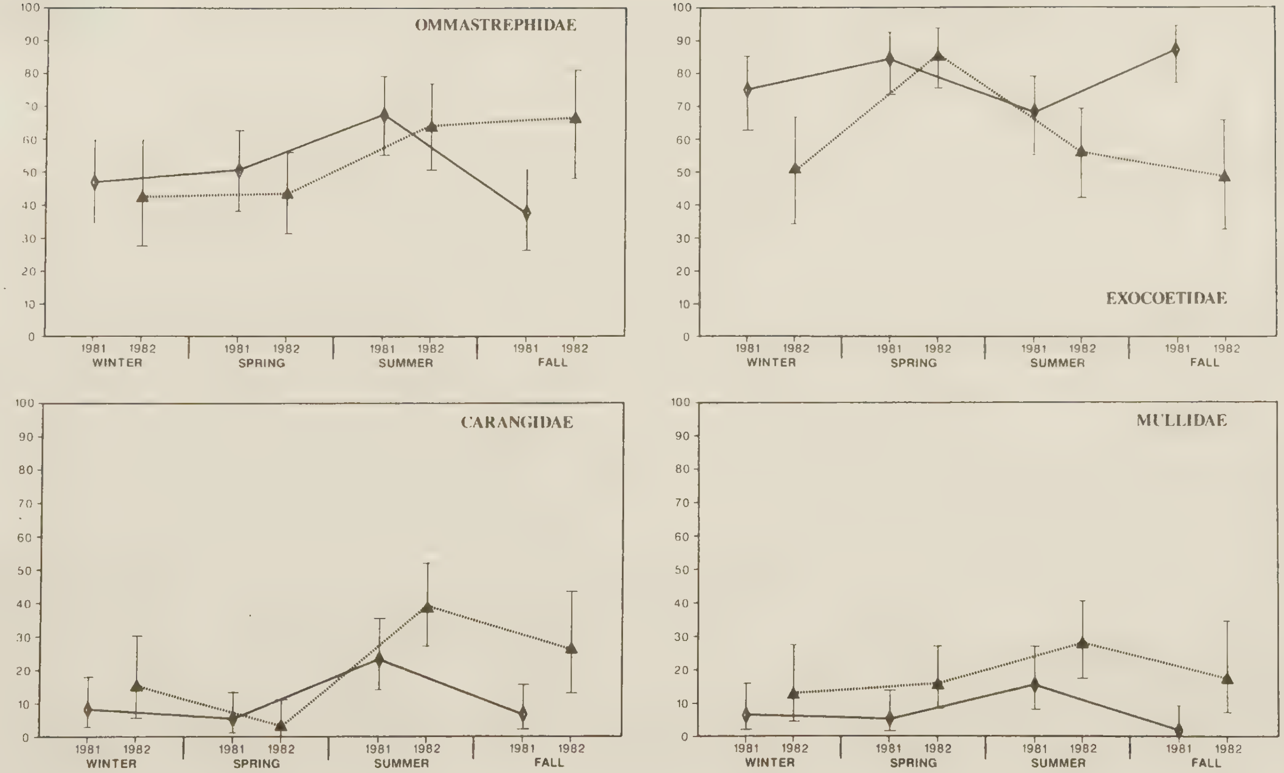

Figure 3. Seasonal frequencies of occurrence and the 95% confidence limits of major red-footed booby prey families at French Frigate Shoals.

(*Euleptorhamphus viridus*). The smallest fish collected was a juvenile flyingfish, *Cheilopogon* sp., at 35 mm SL. Among major prey families, Exocoetidae (N = 64) were 35–188 mm SL ($\bar{x}$ = 134.8, s = 27.8), Mullidae (N = 23) were 38–102 mm SL ($\bar{x}$ = 62.7, s = 18.3), and Ommastrephidae (N = 106) were 11–141 mm ML ($\bar{x}$ = 86.4, s = 22.4).

A total of 261 prey items in condition good enough to obtain accurate weight data were collected. These prey ranged from a juvenile billfish weighing 0.4 g to a flyingfish, *Hirundichthys speculiger*, weighing 97.7 g ($\bar{x}$ = 25.6 g, s = 18.6). Again, we emphasize that both length and weight data collection involved only prey items with minimal digestion. Larger and more digested prey were taken, but accurate measurements were not obtainable and, therefore, not summarized here.

Discussion

Monitoring food habits can be extremely important in assessing the general health and stability of seabird populations (Fefer et al., 1984). Such assessments require the establishment of comprehensive baselines and must overcome a problem common among past seabird diet studies, that is, the inability to obtain samples year-round. This is a reflection of individual phenologies of seabird species, many of which spend much of the year entirely at sea. As mentioned earlier, black noddies and red-footed boobies were selected as our study species primarily because both reside at Tern Island throughout the year. In addition, the feeding ecology of these species could provide valuable insights into fisheries interactions. Our preliminary study indicated that both seabirds relied, at least in part, on fishes targeted for fisheries development (Harrison et al., 1983). Black noddies typically feed nearshore, often in association with jacks (*Caranx* sp.); red-footed boobies are deepwater feeders occasionally found in association with tuna schools.

Our description of the black noddy diet is consistent with prior studies in that fishes form a very high proportion of this species' diet composition (Stonehouse, 1962; Ashmole and Ashmole, 1967b; Diamond, 1983; Harrison et al., 1983). Ashmole and Ashmole (1967b) found 17 fish families accounting for 95% of the number of food items and occurring in 96% of the samples. The major families found in their study at Christmas Island were Exocoetidae (which ranked highest) followed by Scombridae and Blenniidae (ranking equally second). Diamond (1983) found Mullidae (*Upeneus* sp.) to be the most abundant prey item at Cousin Island. The most related study was that conducted by Harrison et al. (1983) in which pooled samples collected at seabird colonies throughout the NWHI showed the highest ranked prey for the black noddy to be mullids, followed by synodontids and clupeids. When considering only those samples collected from French Frigate Shoals, there was no difference from the current study in the highest ranked fish prey; synodontids were by far the highest, followed by mullids and microdesmids. In all of the studies, the only invertebrate found to be of importance to black noddies is the squid family Ommastrephidae (in particular, *Sthenoteuthis* [*Symplectoteuthis*] *oualaniensis*).

Similarly, our results of the red-footed booby diet further document the findings of previous studies conducted at Oahu, Hawaii (Ashmole and Ashmole, 1967a), at Christmas Island (Schreiber and Hensley, 1976), Aldabra Atoll (Diamond, 1974; 1983), and the NWHI (Harrison et al., 1983): The diet of red-footed boobies is composed predominantly of flyingfishes and ommastrephid squids. Ashmole and Ashmole (1967a) found that, in addition to these major prey, snake mackerels were important. Carangidae (primarily *Decapterus* sp.), Mullidae, Scomberesocidae (*Cololabis saira*), and Scombridae were the other highly ranked fish prey families found in pooled samples collected at seabird colonies throughout the NWHI (Harrison et al., 1983). When only the samples collected from French Frigate Shoals were considered, there was no difference in the highest ranked prey families from the current study.

These results suggest that, as with other subtropical seabirds, black noddies and red-footed boobies are apex, opportunistic predators. They apparently will feed on almost anything of appropriate size that becomes available in the surface waters near roosting and breeding areas. Their opportunistic character is evidenced by prey diversity. The 34 prey families taken by black noddies and the 23 prey families taken by red-footed boobies represent very diverse diets when compared to seabird diets in temperate areas (Pearson, 1968) or in Peru where anchovies constituted 80–96% of the seabirds' food (Jordan, 1967). Although many prey families are represented by just a few specimens taken during a single season, these incidental prey are further indicators of an opportunistic predator (Diamond, 1983). These prey may be eaten only when common prey items are scarce, but their presence enables a species to survive during food shortages. Their importance should not be underestimated (Ashmole and Ashmole, 1967b).

Our seasonal analyses lend support to the notion that peak food availability created by natural distribution of prey species is the controlling factor in the timing of seabird breeding. Although most of the seabirds in the NWHI breed in the spring and summer months, black noddies have adapted to a breeding season that begins in the winter (Fefer et al., 1984). It has been proposed that black noddies are able to raise their young in the winter because they feed in association with winter-resident, inshore, predatory fishes; their phenology, however, may be attributed more to the apparent natural fall and winter abundance of synodontids and microdesmids. This is discussed more in detail below. The importance of the dartfish, *Ptereleotris heteroptera,* as a prey item is unique to black noddies among the NWHI seabirds (Harrison et al., 1983). Mullids reportedly spawn during spring-summer in Hawaii (Miller, 1974; Moffitt, 1979) and, hence, the lower occurrence of these juveniles in the fall. Corbin (1977) hypothesized that juvenile mullids have 1.5- to 2-month pelagic stages before settling into their adult benthic habitat. Red-footed boobies breed primarily in the spring-summer but are capable of egg laying throughout the year (Nelson, 1978). Likewise, occurrence frequencies of exocoetids and ommastrephid squids in the booby diet peak in the spring-summer but boobies exploit this resource year-round. The distribution and abundance of flyingfishes reportedly alter with seasonal shifts of sea-surface isotherms (Bruun, 1935; Parin, 1963; 1968; Shuntov, 1968). For subtropical exocoetid species, optimal surface temperatures are 21.5°–26°C (Parin, 1963). Harman and Young (1985) reported that early growth stages of ommastrephid squids were collected throughout the year in Hawaii indicating year-round spawning. Specifically, larval *S. oualaniensis* were found in greatest abundance in the fall. Seasonal prey availability, breeding phenology, and the trophic relationships of the these seabirds are further influenced by their interactions with the local fisheries.

Perhaps the greatest concern involving seabirds is their interrelationships with various aspects of commercial fisheries. It has been well-documented that, in many parts of the world, there is significant competition between seabirds and fisheries (Crawford and Shelton, 1978; Furness, 1982; Safina and Burger, 1985). In the relatively pristine environment of the NWHI, commercial fisheries are still very much in their infancy, and considerable attention is directed towards seabirds and their role in the marine ecosystem as the interest in the exploitation of the resources continues to grow. Prior studies in the NWHI have recognized that seabirds remove significant amounts of energy from the ecosystem. Fefer et al. (1984) reported that NWHI seabirds consume some 410,000 t of marine resources each year, and Polovina (1984) estimated that seabirds consume 42% of the annual production of small pelagic fishes and squid in an ecosystem model of the French Frigate Shoals. Nevertheless, it is difficult to assess what, if any, impact the NWHI seabirds have on commercial fisheries or vice versa, even when they remove such substantial amounts of energy. Tropical ecosystems are complicated by the migratory nature of tuna stocks and other predators on which the birds depend to drive prey to the surface. The juvenile forms of fishes and squid that comprise much of the food consumed by seabirds are below the trophic levels that would directly affect commercial fisheries.

The development of a fishery that exploits coastal pelagic species would have the most significant impact on the natural existence of the seabirds. Both black noddies and red-footed boobies have been identified as species that regularly occurred in flocks feeding in association with predatory fishes (King, 1970; Gould, 1971). A great majority (75.4%) of predatory fish schools found under flocking birds in Hawaii have been identified as skipjack tuna, *Katsuwonus pelamis* (Harrison and Seki, 1987); therefore, the relationship of the birds with this tuna species requires some discussion. The diet composition of Hawaiian skipjack tuna is similar to that of these seabirds (Yuen, 1959; Waldron and King, 1963). The fish families Carangidae (predominantly *Decapterus* sp.), Scombridae, and Mullidae and the squid family Ommastrephidae were the most common prey in both studies. There is obviously some overlap of components with the noddy diet, which includes mullids and ommastrephids among its major components, and with the booby diet, which includes all of these common prey. Although no seasonal analysis was conducted on the tuna feeding studies, skipjack tuna are in greatest abundance during their peak spawning season from May to September (Matsumoto et al., 1984). We can speculate that, if indeed the birds depend on predatory fishes to make the prey available, the major prey of both the fishes and birds should be similar during these months. It is, therefore, not surprising that carangids and mullids are taken most frequently during the spring and summer months by both noddies and boobies and that juvenile scombrids only occur in the bird diets during the summer and fall. Likewise, the overlapping occurrence frequencies of prey families are lowest during the winter months. Size ranges of the major prey taken were also similar between skipjack (Harrison and Seki, 1987) and the birds, which provides further evidence that prey of the seabirds are also probably the forage for tunas. Ashmole and Ashmole (1968) suggested that the lack of flyingfishes in the diets of tunas compared to seabirds is probably due to the ability of these fishes to escape submarine predators by flying and, thus, rendering them vulnerable to aerial predation. For black noddies that also feed in association with inshore resident jacks, there was no overlap in dietary components (Parrish et al., 1980), and it is doubtful that predatory fishes play a major role in the noddies' ability to exploit the large numbers of synodontids and microdesmids in the winter. Such a phenomenon is strictly attributed to a seasonal influx of prey in the ecosystem and the opportunistic predatory ability of the noddies.

In conclusion, although we have furthered our understanding of the trophic ecology of tropical and subtropical seabirds, our limited knowledge of the marine ecology and fisheries of the region prevent further insight into the role of seabirds in the ecosystem. Improvements in our ability to identify postlarval and juvenile fishes and squids will result in refinements in our analyses of dietary specialization. Such a task will not be easy because young stages of fishes and squids are very difficult to sample with even state-of-the-art gear. It is ironic that pelagic seabirds have served as the most effective sampling gear for much of the small nektonic epipelagic fauna. Distributional data of juvenile organisms, such as the ommastrephid squid, *S. oualaniensis* (Young, 1975; Okutani and Tung, 1978), the dartfish, *P. heteroptera* (Randall and Hoese, 1985), and the morwong, *Cheilodactylus vittatus* (Randall, 1983), are based primarily on the collections of seabird food samples. Our results here support the proposition by Ashmole and Ashmole (1968) to use seabird food samples to study seasonal variation of epipelagic fauna of tropical oceanic areas.

We need to improve our knowledge of seabird foraging ranges and locations. This information would be most critical during the incubation and chick-rearing periods when food demands become more localized around nesting areas. Preliminary foraging distances have been inferred from incubation shifts and feeding frequencies of young (Harrison and Hida, 1980), but these estimations are extremely crude, and alternative methods of assessment should be sought. The use of radiotelemetry to identify feeding locations has been employed experimentally on the brown noddy, *Anous stolidus,* a congener of the black noddy (Harrison and Stoneburner, 1981). Use of this technology should be expanded in the future.

Finally, historical studies have failed to incorporate concurrent oceanographic data with diet. Occurrences of major ecological perturbations such as an El Niño Southern Oscillation (ENSO) event have been shown to have significant impacts on diets as well as breeding phenologies of birds in other areas (Schaefer, 1970; Idyll, 1973; MacCall, 1984; Gibbs et al., 1987). Our seasonal analyses of black noddy prey frequencies reveal considerable deviations in the fall 1982 from trends of prior years. Although we did not have concurrent time series of oceanographic and environmental data to examine any pertubations that may have influenced the changes in trends, we could not help but speculate as to the possibility that limited effects of the 1982–1983 ENSO may have had some impact even this far west in the Pacific. Whatever the reason for the variation in diet, breeding populations were not adversely affected as they were at Christmas Island during the same period (Schreiber and Schreiber, 1983; 1984; Gibbs et al., 1987). Obtaining oceanic physical information around the colonies and foraging areas would be most beneficial to the monitoring of seabird populations and to the understanding of the ecosystem dynamics.

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8967

Status of Pacific Billfish Stocks

Robert A. Skillman

With the increasing worldwide importance of recreational fishing for billfishes, interest in the biological status of billfish populations has heightened. The first attempt at assessing their status on a Pacific-wide basis occurred at a workshop held in Honolulu, Hawaii, U.S.A., in 1977 (Shomura 1980). Indian Ocean billfish stocks were included in a 1979 stock assessment workshop held in Shimizu, Japan (FAO 1980).

This chapter updates the assessments of Pacific billfish by including both more recent data and logbook data from Korea and Taiwan. Additional objectives include determining whether Korean and Taiwanese data can be used to extend the assessment beyond 1980, when Japanese logbook data ceased being published, identifying gaps in the data, and pinpointing other shortcomings in the analyses of individual species. Species included in the study are Indo-Pacific blue marlin *(Makaira mazara)*, black marlin *(M. indica)*, striped marlin *Tetrapturus audax)*, Indo-Pacific sailfish *(Istiophorus platypterus)*, shortbill spearfish *(T. angustirostris)*, and swordfish *(Xiphias gladius)*.

The present assessments are based on a generalized production model (Pella and Tomlinson 1969), analysis of catch rates derived from logbooks, and total catch estimates from volumes of the *Yearbook of Fishery Statistics* published by the FAO (1947-). Steps in the analysis involve (1) selection of probable stock boundaries; (2) selection of index areas for computing estimates of abundance; (3) computation and comparison of these catch rates based on Japanese, Korean, and Taiwanese logbook data; (4) estimation of effective fishing effort; and (5) computation and evaluation of surplus production model estimates of maximum sustainable yield (MSY) and optimum fishing effort at MSY (f_{opt}). The following sections describe the data sources and the steps listed above.

Data Sources

Two basic types of data are used in this study, namely catch-and-effort statistics and estimates of total catch. The former is derived from logbooks and includes estimates of nominal fishing effort and the resulting number of billfishes caught by the Japanese, Korean, and Taiwanese tuna longline fisheries. Unpublished Japanese data for 1952-1961 were provided by the Far Seas Fisheries Research Laboratory (7-1, 5 Chō me Orido, Shimizu 424, Japan) in 1977, whereas data for 1962-1980 are based on logbook statistics published by the Fisheries Agency of Japan, Research Division. Korean data for 1966-1970 and 1975-1982 are based on statistics published by the National Fisheries Research & Development Agency. Lastly, Taiwanese data for 1967-1979 and 1983-1984 were taken from computer listings provided by the Institute of Oceanography, National Taiwan University (P.O. Box 23-13, Taipei, Taiwan, Republic of China).

The second type of data, namely total catch data in metric tons (t), is derived from volumes of the *Yearbook of Fishery Statistics* published by the FAO. These data are the official, total catch statistics submitted by the nations for their flag vessels. Statistics for the early years used in this study are actually modifications of the FAO statistics made during the 1977 workshop (Shomura 1980). Participants agreed upon species estimates of total Pacific catch for 1952-1963, when FAO statistics were not presented by ocean, and also of separate estimates for blue and black marlins for a few years when FAO published only combined statistics. The total catch data used in this study appear in Table 1 and include updates from recent FAO yearbooks.

Stock Structure

To determine stock structure and to select index areas for computing stock abundance, basic information on the distribution and stock structure of each of these billfishes was extracted from Nakamura (1974) and Shomura (1980). This information was supplemented with annual and quarterly plots of the geographical distribution (5° rectangles) of Japanese catch, fishing effort, and catch rates (simple ratios of annual catches and fishing effort) (unpubl. data).

Indo-Pacific Blue Marlin

In the Pacific Ocean, blue marlin appear to consist of a single stock centered about the Equator, with the poleward extent of its distribution varying seasonally (Shomura 1980). The highest catch rates typically occur along the Equator; high catch rates also occur with varying degrees of regularity in subtropical waters. Thus, I selected five potential index areas (Fig. 1): area 1 has the longest history of higher catch rates and substantial fishing effort, area 4 has a less consistent temporal distribution of fishing effort, and areas 2, 3, and 5 have substantial catches and catch rates in some years. Based on catch rates by index areas (Fig. 2), I selected area 1 for computing indices of stock abundance, although areas 3 or 4 could also have been used. Catch rates for the entire Pacific and area 2 (not shown in Figure 2 to remove clutter) are low throughout the time series and show little or no trend.

Black Marlin

The stock structure of black marlin is not known but may comprise several stocks on the eastern and western rims of the Pacific (Shomura 1980), and there may be exchange between Pacific and Indian Ocean stocks (FAO 1980). The distribution of catch rates suggest a single stock centered off Australia, with the species being widely distributed but not consistently abundant elsewhere. Hence, I set up four potential index areas (Fig. 1) and compared their catch rates (Fig. 2). Based on these results, and for lack of clear evidence to the contrary, I assume a single, Pacific-wide stock for the remainder of this analysis and use area 2 as the stock index area.

Table 1 Total Pacific billfish catch (in metric tons) by species and FAO statistical areas, 1952-85. Data were derived from Shomura (1980) and volumes of the Yearbook of Fishery Statistics *published by the Food and Agriculture Organization of the United Nations.*

			Striped Marlin						**Sailfish–Shortbill Spearfish**					
Year	Blue marlin	Black marlin	61	71	77	81+87	All	Swordfish	61+67	71	77	81	87	All
1952	15.525	1.806					4.992	11.339						2.000
1953	17.250	3.188					3.789	11.689						3.300
1954	10.519	5.370					7.256	13.392						2.400
1955	24.190	5.379					7.075	16.485						3.300
1956	18.770	6.466					7.724	12.584						3.200
1957	23.500	6.376					7.150	16.243						2.800
1958	22.106	4.548					8.999	21.341						3.400
1959	20.275	3.081					8.986	19.663						3.400
1960	18.155	2.721					7.362	23.409						5.000
1961	26.581	3.170					10.084	24.286						4.800
1962	30.743	4.066					13.685	14.604						6.800
1963	31.344	3.180					16.944	14.113						7.900
1964	23.233	2.805					23.480	10.112	3.700		2.100	300	0	6.100
1965	18.885	4.039	12.700		11.700	1.600	26.000	12.949	3.600		9.100	0	100	12.800
1966	18.588	3.729	9.600	1.900	9.500	3.500	24.500	14.601	3.800	1.200	5.900	0	100	11.000
1967	17.233	2.836	8.300	1.700	10.800	1.600	22.400	15.649	3.300	1.400	6.900	0	100	11.700
1968	15.283	2.362	10.200	1.200	11.400	2.700	25.500	15.230	4.800	400	6.100	0	1.200	12.500
1969	17.427	2.546	11.900	900	8.900	2.900	24.600	18.934	4.900	300	6.900	0	700	12.800
1970	20.115	2.207	11.000	1.300	11.100	2.400	25.800	15.727	3.700	300	4.900	0	200	9.100
1971	13.342	2.674	12.300	700	11.200	2.100	26.300	11.037	2.500	500	4.900	200	200	8.300
1972	15.300	3.424	3.800	800	7.600	2.000	14.200	11.029	2.000	800	5.700	0	100	8.600
1973	17.285	3.400	6.600	1.000	5.900	1.700	15.200	15.100	2.800	900	4.900	0	100	8.700
1974	15.594	2.665	6.287	591	5.846	2.176	14.900	14.622	1.959	539	5.153	57	29	7.737
1975	12.546	3.613	9.258	560	5.426	1.959	17.203	16.409	3.373	362	3.620	117	32	7.504
1976	12.611	3.086	5.676	328	5.961	2.034	13.999	19.322	2.708	514	10.187	32	29	13.670
1977	13.819	2.737	7.420	207	3.353	1.312	12.292	18.318	5.079	346	5.797	119	50	11.391
1978	15.998	3.796	8.472	691	2.507	1.263	12.933	18.032	3.778	851	5.425	40	31	10.125
1979	16.656	3.530	5.749	717	4.776	2.541	13.783	19.179	2.805	322	4.351	87	40	7.605
1980	19.029	2.120	7.454	904	5.134	2.292	15.784	16.616	5.209	449	1.535	78	56	7.327
1981	13.378	2.136	6.748	901	5.715	1.493	14.857	18.937	3.960	566	566	139	26	5.257
1982	15.398	1.712	4.822	1.194	5.193	2.964	14.173	18.649	2.603	537	2.259	241	58	5.698
1983	14.317	2.216	4.355	664	3.949	1.715	10.683	18.770	3.687	436	1.828	116	78	6.145
1984	14.149	1.577	5.980	589	3.141	980	10.690	18.161	2.988	487	1.270	108	[illegible]	4.790
1985	12.609	1.572	6.766	1.108	2.307	850	11.031	19.468	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	4.274

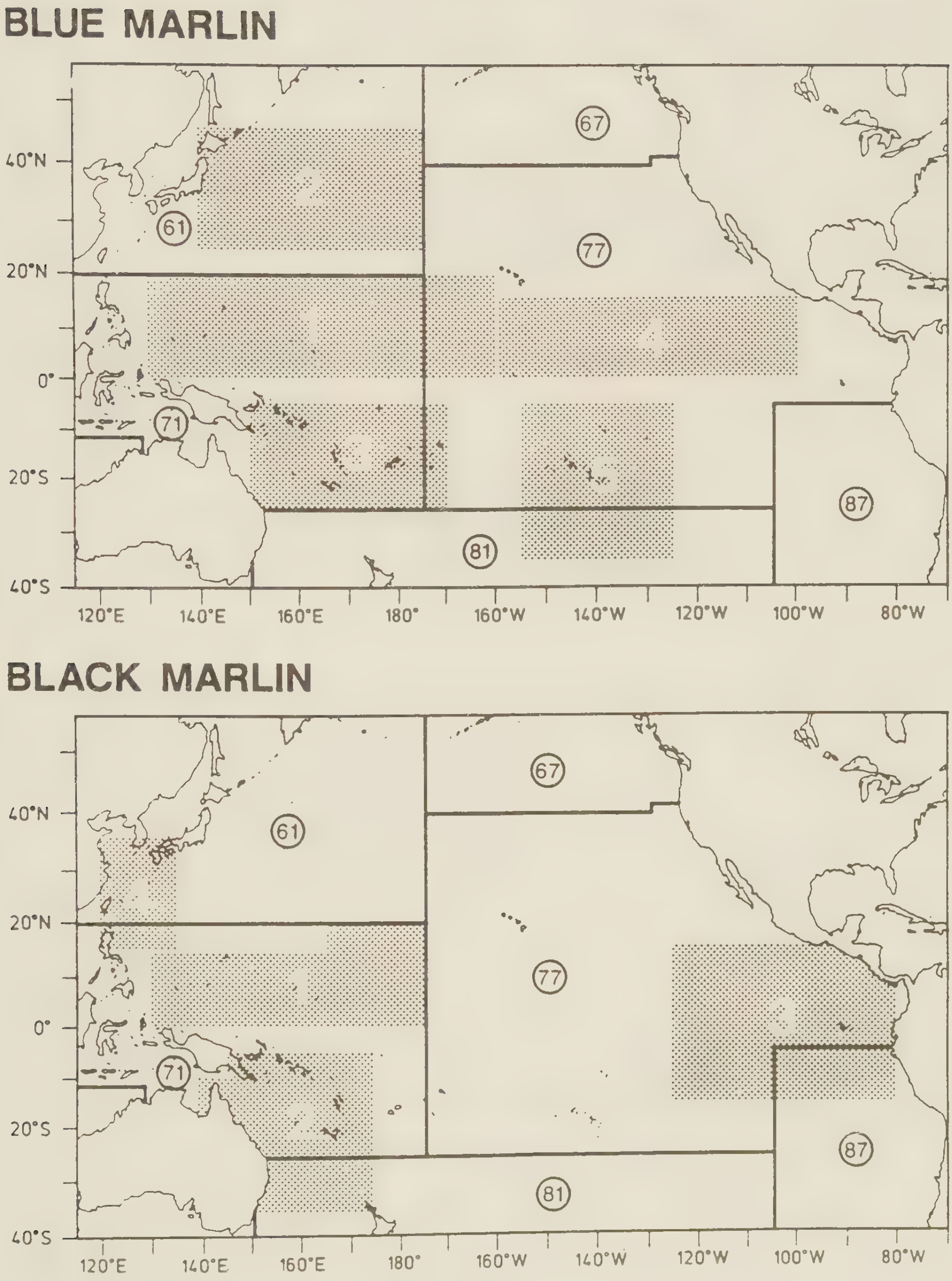
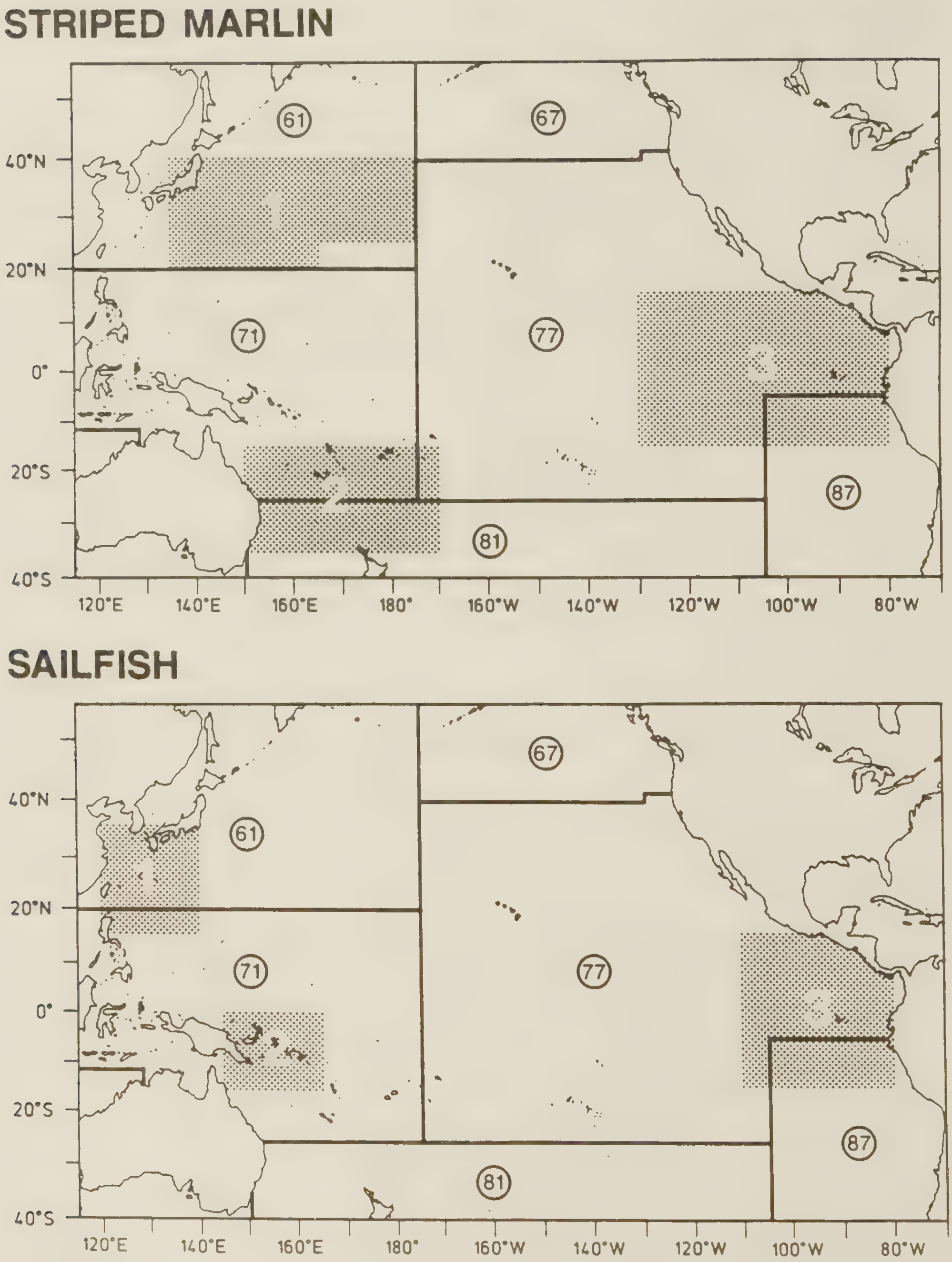


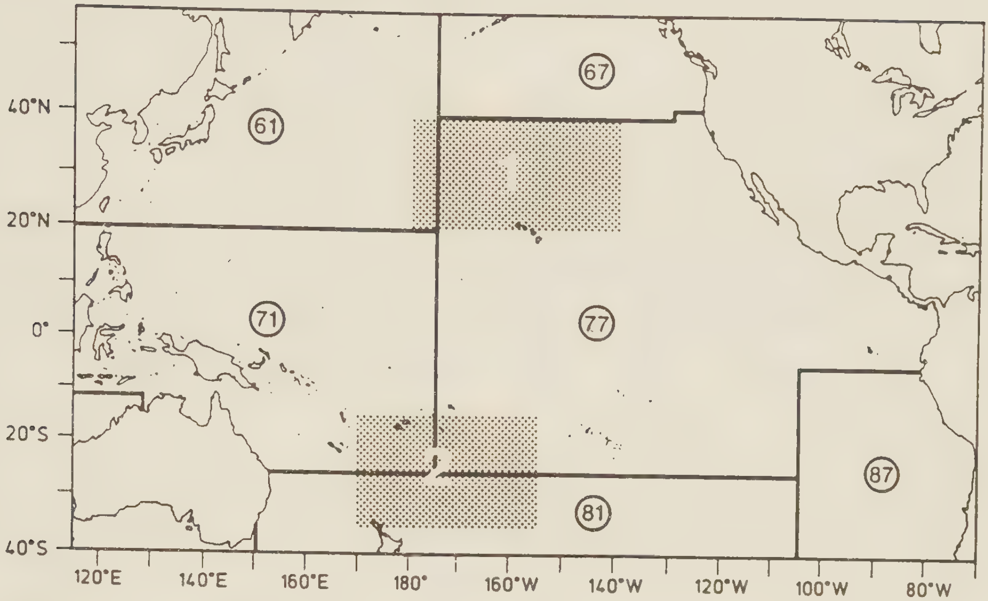
Figure 1. Index areas and Food and Agriculture Organization of the United Nations statistical areas.


STRIPED MARLIN

SAILFISH

Figure 1. Index areas and Food and Agriculture Organization of the United Nations statistical areas.

SHORTBILL SPEARFISH



SWORDFISH

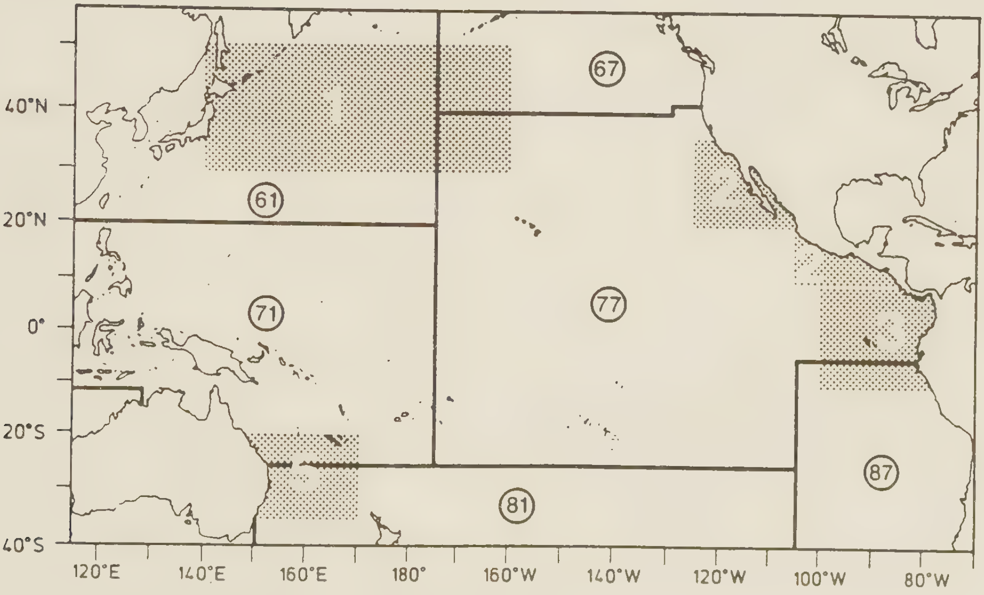


Figure 1. Index areas and Food and Agriculture Organization of the United Nations statistical areas.

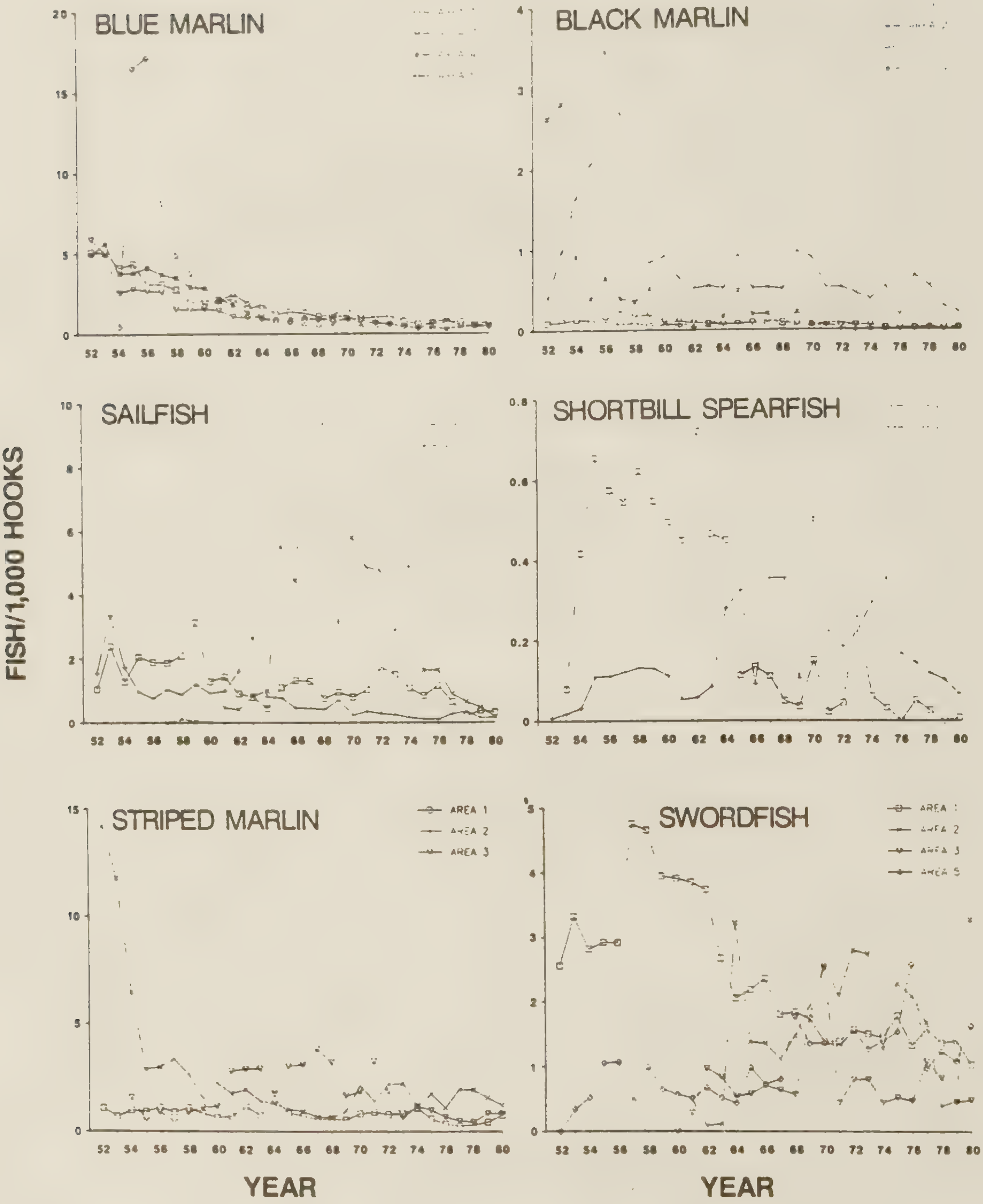


Figure 2. Historical trends in billfish catch rates by index areas.

Striped Marlin

Striped marlin may be composed either of separate north and south stocks or a single Pacific-wide stock (Shomura 1980). Consistent with either view is the distribution of catch rates, which are consistently high in the northern central Pacific, often in the southern central Pacific (frequently during the same quarters of the year), and also in eastern tropical Pacific waters on both sides of the Equator. Thus, I selected three potential index areas (Fig. 1) and compared the catch rates over time (Fig. 2). The catch rates in areas 1 and 2 are not correlated, but those in area 3 are negatively correlated with those in area 2 ($P < 0.05$). Thus, some evidence of separate north and south stocks exists, and assessment of this species was attempted accordingly.

Sailfish and Shortbill Spearfish

Very little is known about the stock structures of sailfish and shortbill spearfish. Assessment is difficult because statistics for the two species are reported together in both the distant-water logbook data and the FAO yearbooks. Sailfish are abundant along the American and Asian rims of the Pacific, indicating separate eastern and western stocks (Shomura 1980). Information presented by Nakamura (1974) suggests two western Pacific stocks. Based on these hypotheses, I set up three index areas (Fig. 1) and compared catch rates (Fig. 2), assuming the catch rates in these coastal areas represent mostly sailfish abundance. Because the three areas show dissimilar trends, I concluded there are three separate stocks.

Spearfish have a more oceanic distribution than sailfish and appear to have separate northern and southern central Pacific stocks. Based on this conjecture, I set up two potential index areas (Fig. 1) and compared the catch rates (Fig. 2), assuming catch rates in these pelagic areas represent mostly spearfish abundance. The two areas show dissimilar catch rate trends, thus lending support to the two-stock hypothesis.

Swordfish

Swordfish may consist of a single, Pacific-wide stock or northwestern, southwestern and eastern Pacific stocks (Shomura 1980). Plots of catch-rate data suggest a single stock centered in the northwest Pacific that extends over the entire Pacific at lower densities; higher catches occur in some coastal fisheries. After setting up four potential index areas (Fig. 1) and comparing their catch rates (Fig. 2), I concluded that swordfish consist of a single Pacific-wide stock and used area 1 as the index area.

Extending the Time Series

The Japanese catch-and-effort statistics, which have served as the mainstay of stock assessment efforts for tunas and billfishes, are no longer published. Therefore, I explored whether Korean and Taiwanese tuna longline statistics could be used to extend the Japanese time series beyond 1980. This evaluation was conducted for each species by plotting the annual ratio of average catch rate (fish/1,000 hooks) for the selected index area and by calculating the coefficient of correlation for the years of overlap among the different national data series. The interrupted nature of the Korean and Taiwanese data complicates the interpretation of the results; also, these countries entered the tuna longline fishery after much of the decline in abundance of billfishes had occurred.

Starting with blue marlin in index area 1 (Fig. 3), the time series for Japan and Korea are significantly correlated ($r=0.767$, $P < 0.05$), while other possible comparisons are not significant ($r=-0.241$, Japan-Taiwan; $r=0.024$, Taiwan-Korean; $P > 0.05$). Paired *t*-tests show, as expected, that the catch rates for Japan are significantly higher than those for Korea and Taiwan ($t=7.517$ and 3.863, respectively; $P < 0.01$), while those for Korea and Taiwan are not significantly different ($t=2.138$, $P > 0.05$). These statistics indicate that Korean data could be used to extend the time series by 2 years, but they must be scaled to the Japanese time series.

For black marlin in index area 2 (Fig. 3), none of the time series is significantly correlated ($r=-0.502$, Taiwan-Japan; $r=-0.756$, Korea-Taiwan; $r=-0.568$, Japan-Korea; $P > 0.05$). Korean and Taiwanese data cannot be used to extend the Japanese time series.

For striped marlin, I compared the statistics by using a composite of index areas 1, 2, and 3, rather than each area separately (Fig. 3). As with blue marlin, the Japanese catch rates were significantly greater than those for Korea and Taiwan (paired *t*-test = 6.836 and 8.289, respectively; $P < 0.01$), but were correlated with those for Taiwan ($r=0.654$, $P < 0.05$) rather than Korea $r=0.040$, $P > 0.05$). Thus, the Taiwanese data could, once scaled, be used to extend the time series; however, a 3-year gap

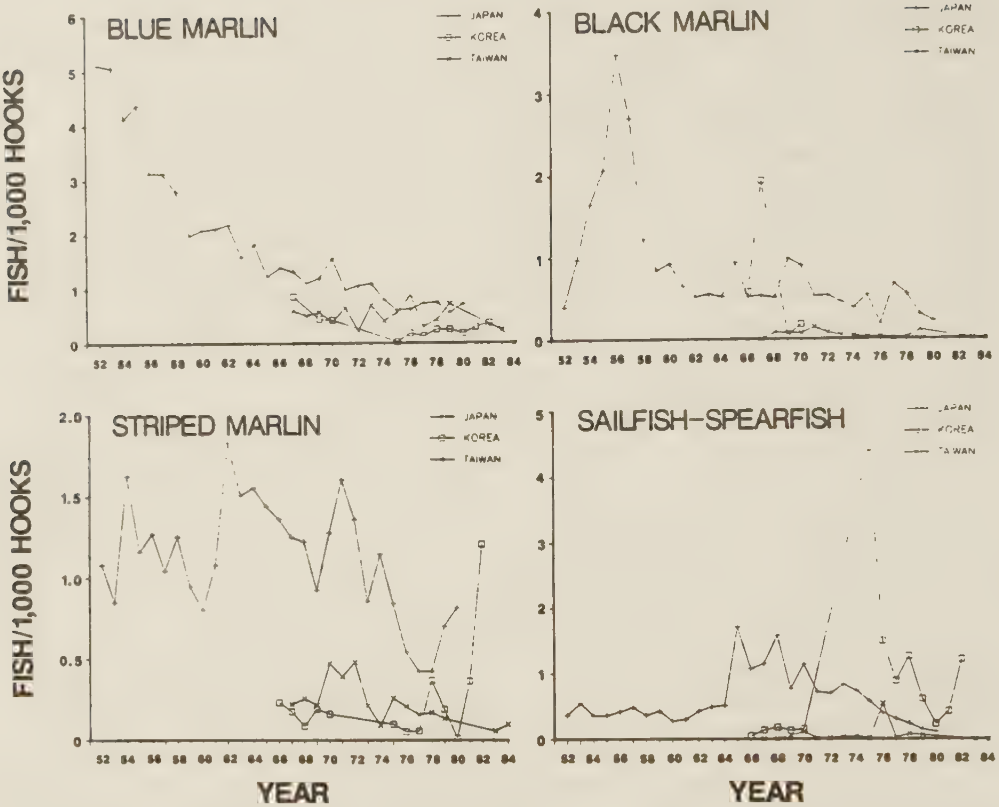


Figure 3. Comparison of Japanese, Korean, and Taiwanese catch rates of blue marlin (index area 1), black marlin (index area 2), striped marlin (index areas 1, 2, and 3 combined), and sailfish-shortbill spearfish (entire Pacific).

exists between the end of the Japanese time series and the last two Taiwanese data points.

For sailfish and spearfish combined, the catch rate trends are quite dissimilar (Fig. 3), indicating that neither Korean nor Taiwanese data can be used to extend the Japanese time series.

For swordfish in index area 1, Taiwan reported catches for only 1 year, and the Japanese and low Korean catch rates are quite dissimilar. For a composite of all the potential index areas, none of the time series is correlated ($r = 0.377$, Japan-Korea; $r = 0.211$, Japan-Taiwan; $r = 0.654$, Korea-Taiwan; $P > 0.05$). Thus, Korean and Taiwanese data cannot be used to extend the time series.

Based on these results, the Korean and Taiwanese data for billfishes are not of sufficient quality to extend the published Japanese time series. A couple of significant correlations out of 16 comparisons is not sufficient to convince me that these data can be used to assess the status of any of the billfish stock.

Some Conversions Before Fitting the Production Model

The most straightforward situation in fitting the surplus production model is when one has a complete time series of estimates of fishing effort and the resultant weight of fish caught. This situation rarely, if ever, exists. While reasonably good estimates of the weight of the various billfishes caught are available, catch-and-effort statistics are available for only the generally predominant fishing method (tuna longline) and then effectively for only one of the nations (Japan). Thus, I followed the common procedure of computing catch rates from available catch-and-effort statistics, dividing

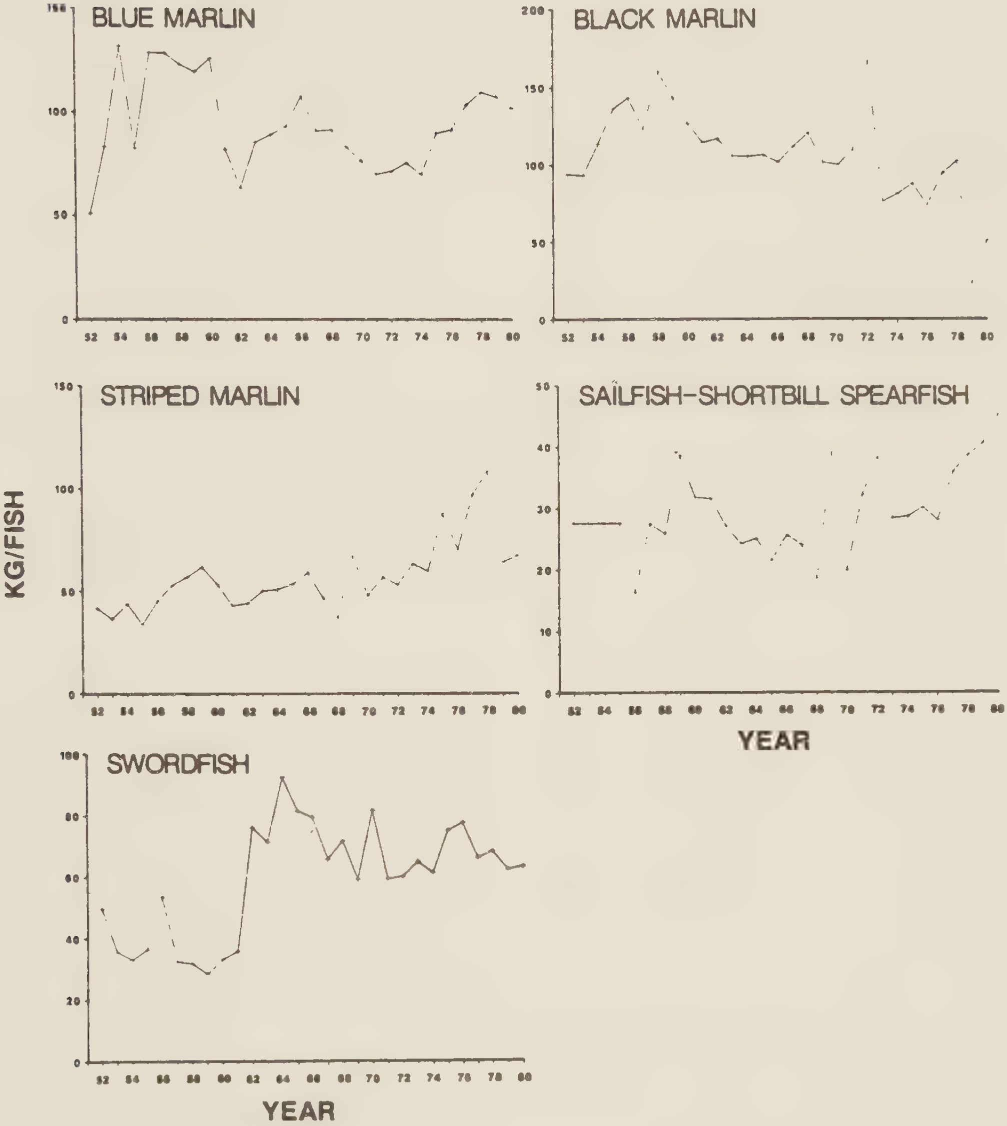


Figure 4. Billfish average weight statistics.

this rate into total catch to obtain an estimate of the total effective effort and then using the estimated total effective effort and total catch to assess the stock. To use this procedure for billfishes (and tunas, for that matter), catch rates must be converted from number of fish per 1,000 hooks to the weight units used for the total catch estimates.

Average Weights

Average weight statistics used to convert the catch rates from number of fish per 1,000 hooks to weight per 1,000 hooks were calculated as follows. Estimates of the number of fish caught, from the Japanese logbook data, were raised to the estimated total number of fish caught for all nations, based on the percent Japanese contribution to the total catch in weight reported for all nations in the FAO yearbooks. This estimate of total number of fish caught was then divided into the FAO estimate of total weight (in metric tons) to estimate average weight. Since this can be done only for the FAO statistical areas, or for the entire Pacific Ocean, it is not possible to assess the status of some of the hypothesized stocks and modifications had to be made for others.

Indo-Pacific Blue Marlin. The trend in Pacific-wide average weight statistics for blue marlin (Fig. 4) appears reasonable, except possibly at the start and end of the series. At the start of the series, the values appear lower than expected from the trend following. After 1975, average weight increases; this change in trend could be caused by reduced fishing pressure, changes in fleet make up or fishing strategy, or even diminished recruitment due to random events or excessive fishing pressure.

Black Marlin. Estimated average weight of black marlin for the entire Pacific follows a downward trend, particularly in the last few years (Fig. 4). Again, average weight in the first few years in the series appears to be too low given the remainder of the series.

Striped Marlin. For striped marlin, the average size statistics using Pacific-wide data (Fig. 4) show an increasing trend throughout the history of the fishery. Since this trend is the opposite of that expected for heavily exploited stocks, the reliability of the statistics and the validity of any production model fit to the data are suspect. Such a trend might be due to changes in fleet make up or fishing strategy, mismatching (in time) of the logbook and total catch data, or underreporting of tuna longline logbook data. Suzuki (pers. commun.) notes that changes in the average size statistics coincide with increases in the drift-net fishery targeting striped marlin off Japan.

Sailfish-Shortbill Spearfish. The combined reporting of sailfish and shortbill spearfish total catches by FAO and the distribution of the index areas for sailfish and spearfish with respect to the FAO statistical areas (Fig. 1) make average weight statistics impossible to compute for either species. Thus, average size statistics are computed on a Pacific-wide basis for the two species combined. The statistics are variable but show no obvious trend, except for the last several years when sizes increased (Fig. 4).

Swordfish. The average weight trend (Fig. 4) for swordfish on a Pacific-wide basis exhibits a discontinuity between 1961 and 1962. This is when Japan changed to a new statistical system, and about when day setting of longline gear in the Japanese swordfish fishery replaced night setting. After 1962, the trend is gradually toward smaller sizes, which is consistent with a stock exposed to increased fishing pressure.

Effects of Deep Longlining Gear

Use of deep longlining gear, which is designed to place more hooks in deeper water where bigeye tuna and albacore are most abundant, began in about 1974 and increased thereafter. This trend resulted in problems in assessing billfishes. The gear is less efficient at capturing surface-dwelling billfishes (Suzuki and Warashina unpub.), so lower billfish catch rates could be due to use of this gear. The efficiency of deep longling gear has been determined for most billfishes, but the relative proportions of deep and traditional longline gear used have not been documented for any of the distant-water fishing fleets. Thus, a direct means of correcting the catch rate statistics is not available, but it is possible to simulate different scenarios.

Assuming that deep longlining gear was first introduced into the fishery in 1974, and that its use increased slowly at first and then more rapidly by 1980, I examined two hypothetical situations. In the first, the efficiency of the total longline fishery for catching billfish was reduced by 25% by 1980 and, in the second, by 50% (Table 2). These relative efficiency factors were divided into the annual catch rate statistics, and then these adjusted abundance estimates were used, along with the corresponding adjusted estimates of effective effort, to fit the surplus production model.

Table 2. Two scenarios for the effect of deep longline gear on the catch rates of billfishes: i.e., 25% and 50% less than what the catch rates would have been if traditional longline gear had been used exclusively.

Year	25%	50%
1973	1.0	1.0
1974	0.97	0.95
1975	0.94	0.90
1976	0.91	0.85
1977	0.88	0.80
1978	0.84	0.70
1979	0.80	0.60
1980	0.75	0.50

Equilibrium Approximation

To approximate equilibrium conditions, estimated effective effort was adjusted according to the method of Gulland (1969). That is, for each species, the annual effective effort was replaced by the average of that year's effort and k - 1 preceding years, where k is the number of years a year-class was reckoned to contribute significantly to the fishery.

Surplus Production Modeling

The generalized surplus production model in the form of

$$Y/EF = (MSY/f_{opt})\ [m + (1\text{-}m)\ (EF/f_{opt})]^{1/(m-1)}$$

(Wetherall and Yong 1984) — where Y/EF = catch rate or index of abundance (kg/1,000 hooks), EF = adjusted effective effort (in millions of hooks), and m = the shape parameter of the production curve — was fit by nonlinear least squares to obtain estimates of MSY, the optimum level of fishing effort at (f_{opt}) MSY, and the shape parameter (m). In addition, MSY and f_{opt} were estimated with m fixed at 0 (which assumes that catch rate versus effort curve is concave and that the yield curve is asymptotic), at 1 (since m cannot exactly equal 1, I used 1.0000001; the catch rate curve is slightly concave and the yield curve is skewed) and at 2 (catch rate curve is a straight line and the production curve is symmetrical).

Indo-Pacific Blue Marlin

For blue marlin, I used running averages of 2, 3, and 4 years on the effective effort statistics to approximate equilibrium conditions. Duplicate effort values were added to the beginning of the time series to preserve the number of years used in the assessment. However, since the results differed little, only that for the 3-year effort averaging is presented (Table 3). Although the gear effectiveness adjustments shifted the post-1974 data points from the extreme right side of the production curve progressively more to the left, the effect of these adjustments on the parameter estimates was much less than the effect of m. When m was allowed to vary freely, the nonlinear fitting procedure rarely converged. When convergence did occur, the parameter estimates and the regression mean square were lower than when m was fixed at 1 or 2. When m was set at 0, convergence did not occur. The parameter estimates differed little (<1,900 t for 25% gear effectiveness) whether m was fixed at 1 or 2, undoubtedly because of the relatively flat shape of the production curve (Fig. 5). The MSY appears to be about 20,000 to 24,000 t with f_{opt} at about 100 to 140 million hooks.

Table 3. Surplus production model parameter estimates for blue marlin, $k = 3$.

m	MSY (in metric tons)	f_{opt} (in millions of hooks)	Regression mean square
	Unadjusted		
Free 0.3	19,246	70.9	240.9
Fixed 0.0	No solution		
Fixed 1.0	21,734	105.6	361.2
Fixed 2.0	23,757	141.4	360.6
	25% Gear Efficiency		
Free	No solution		
Fixed 0.0	No solution		
Fixed 1.0	21,589	103.0	365.6
Fixed 2.0	23,468	134.6	365.0
	50% Gear Efficiency		
Free	No solution		
Fixed 0.0	No solution		
Fixed 1.0	21,478	103.1	370.6
Fixed 2.0	23,265	133.5	370.1

Black and Striped Marlins

No attempt was made to fit a surplus production model for black marlin because total catch data did not vary with increasing effective effort (Fig. 6).

I attempted to fit the surplus production model (k = 4 for equilibrium averaging) to the striped marlin data, but no solution could be found for any of the shape parameter or gear efficiency adjustments. The production data are too linear for the model to be successfully fit (Fig. 6).

Sailfish-Shortbill Spearfish

Effort was smoothed over 2 years to approximate equilibrium conditions. The gear efficiency adjustments have a substantial effect on the parameter estimates, increasing both the estimates of MSY and f_{opt} (Table 4). The production curve (Fig. 5) suggests that the composite

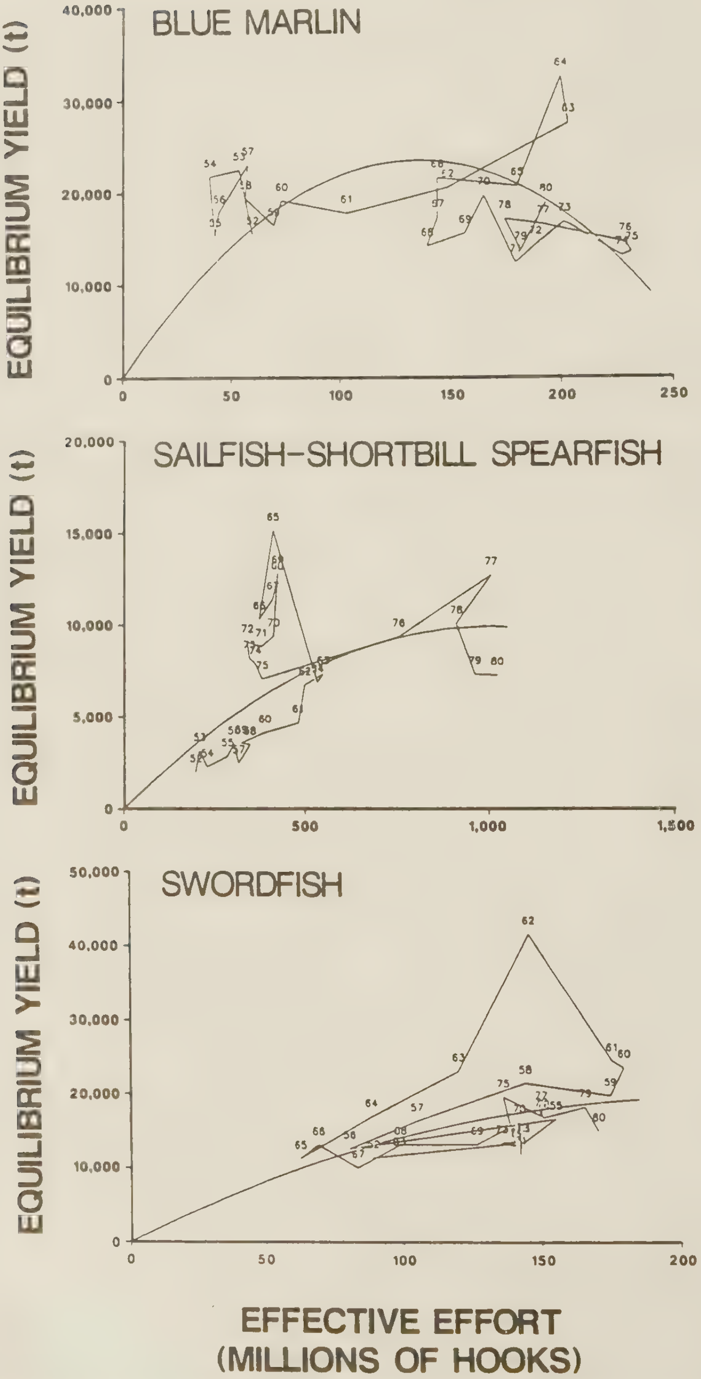


Figure 5 Surplus production using 25% gear efficiency model curves with observed (smoothed and adjusted data for blue marlin ($k=3$, $m=2$), sailfish-shortbill spearfish ($k=2$, $m=2$), and swordfish $k=1$ and 4, $m=2$).

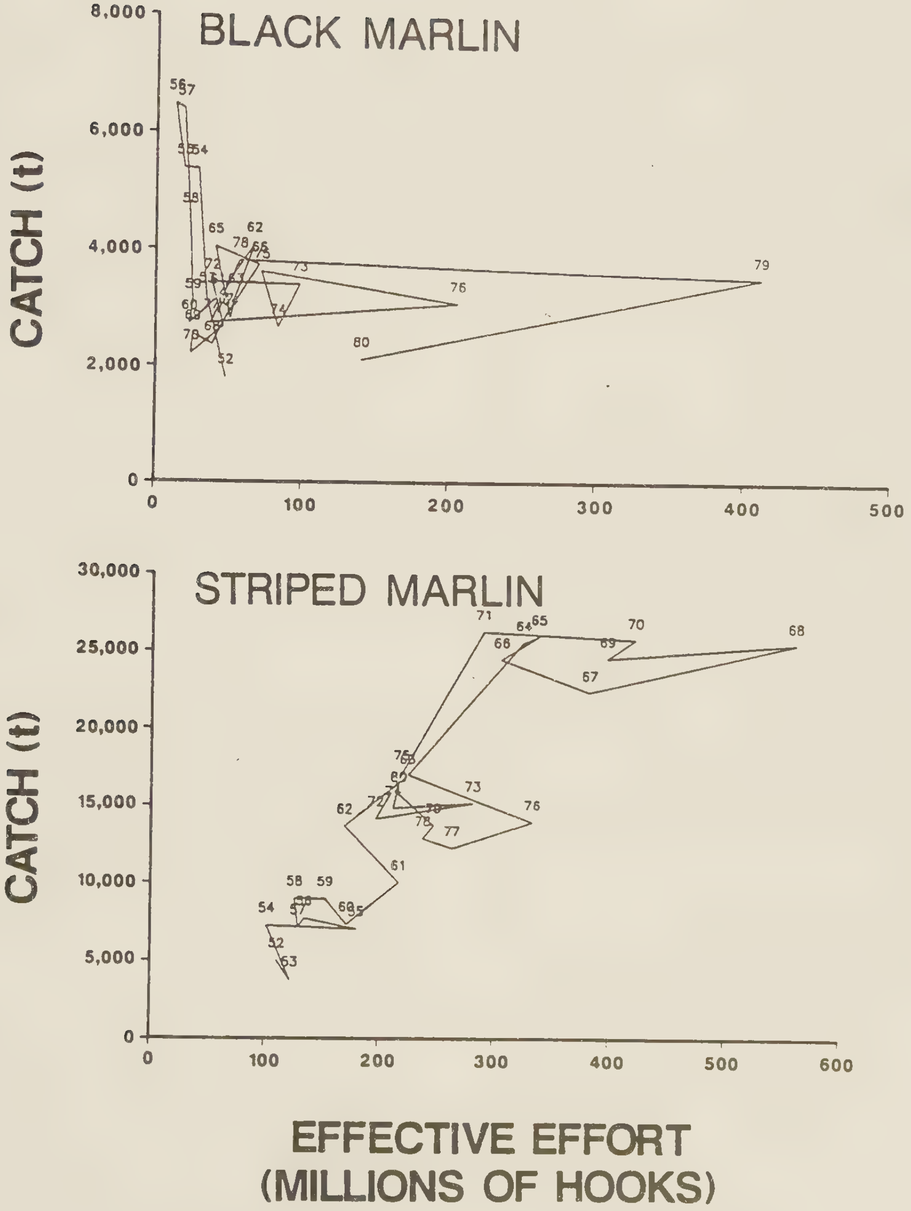


Figure 6. Production model data for black and striped marlins, assuming 25% gear efficiency

fishery for these two species is still on the ascending limb.

Table 4. Surplus production model parameter estimates for sailfish and shortbill spearfish combined, $k=2$.

m	MSY (in metric tons)	f_{opt} (in millions of hooks)	Regression mean square
	Unadjusted		
Free 3.0	10.361	954.7	69.5
Fixed 0.0	19.010	∞	104.0
Fixed 1.0	9.903	1.253.6	104.1
Fixed 2.0	9.608	954.8	104.2
	25% Gear Efficiency		
Free 3.0	9.686	876.3	70.9
Fixed 0.0	26.091	∞	106.3
Fixed 1.0	11.585	1.562.3	106.3
Fixed 2.0	9.884	1.000.0	106.4
	50% Gear Efficiency		
Free 3.0	13.492	1.322.9	72.7
Fixed 0.0	68.919	∞	109.0
Fixed 1.0	24.708	3.860.4	109.0
Fixed 2.0	16.762	1.907.5	109.0

Swordfish

Fishing effort was not averaged from 1952 through 1961, when the Japanese night fishery predominated and the average size was small (Fig. 4); thereafter, a k value of 4 years was used to approximate equilibrium conditions. The adjustments for gear efficiency had a large effect on the parameter estimates, generally increasing estimates of both MSY and f_{opt} while decreasing the shape parameter estimate (Table 5). When m was fixed at 0, valid solutions did not result. As the value of m decreased (whether fixed or estimated), the estimates of MSY and f_{opt} increased. The Pacific-wide stock of swordfish appears to be in good health, with the fishery operating at about the MSY level (Fig. 5).

Table 5. Surplus production model parameter estimates for swordfish, $k=1$ through 1961 and $k=4$ thereafter.

m	MSY (in metric tons)	f_{opt} (in millions of hooks)	Regression mean square
	Unadjusted		
Free 3.0	17.852	167.5	224.0
Fixed 0.0	27.952	∞	335.9
Fixed 1.0	18.219	219.5	335.9
Fixed 2.0	17.703	176.8	336.0
	25% Gear Efficiency		
Free 0.3	24.274	588.9	227.0
Fixed 0.0	34.677	∞	340.6
Fixed 1.0	20.583	274.4	340.6
Fixed 2.0	19.266	206.7	340.6
	50% Gear Efficiency		
Free 0.4	27.217	574.8	230.6
Fixed 0.0	43.126	∞	345.8
Fixed 1.0	23.765	335.6	345.8
Fixed 2.0	21.543	239.1	345.8

Discussion

Indo-Pacific Blue Marlin

Fitting the surplus production model was more successful with the blue marlin data than with data for any other species. In contrast to the other situations, the fishery for blue marlin has gone through a developmental phase, passed the MSY level, and tested the downward limb of the production curve. Use of the equatorial western Pacific index area for calculating catch rate is supported by the successful fit of the model. The large deviation of the 1963-1964 data points from the production curve (for the unsmoothed data, 1962-1963) is notable since the fishery apparently first exceeded the MSY level at about that time. If these data are in error, it is an inopportune time with respect to fitting the model. Since 1975, the adjusted, estimated effective effort statistics have declined, and yield has increased slightly, indicating some recovery of the stock. This view is also supported by the increase in average weights (Fig. 4).

The blue marlin stock still appears to be overfished, with more effort expended than is needed to take the MSY. The situation improved during the late 1970s, and further improvement should occur with the continued decline in the tuna longline fleets and increased use of deep longline gear. Given the corresponding increase in the tuna purse-seine fleets, which catch billfish incidentally, more current longline and purse-seine data are needed to monitor stock condition and to determine fishery interactions. The increase in average weight of blue marlin and the estimated decrease in effective longline effort should be welcome news to recreational fishermen and managers alike.

Black Marlin

From the shape of the catch-rate time series plot (Fig. 2) and the average size statistics (Fig. 4), the lack of a relationship in the production model data is surprising (Fig. 6). With these data, assessing the status of the stock is not possible. Independently derived catch-rate data should be sought since, even by billfish standards, black marlin are an incidental or rare species in the tuna longline fisheries, and catch rate computed from these statistics may not be a good index of abundance. In addition, total catch statistics may be underestimates because of continuing problems in the separation of black and blue marlins in the statistics submitted to FAO (Suzuki pers. commun.).

Striped Marlin

The fishery, assuming a single Pacific-wide stock, reached its highest level of development during the late 1960s and early 1970s, but it is still operating on the ascending limb of the production curve. Post-1974 data seem to fall in the middle of the ascending limb, particularly after adjusting for the use of deep longline gear. Thus, the Pacific fishery for striped marlin is apparently still in the development stage, and the MSY level has not yet been approached by the fishery. In fact, the pressure on the stock in the late 1970s to 1980 appears to have been less than in the late 1960s.

The increasing trend in the average size statistics (Fig. 4) casts doubt on the quality of the statistics and may have led to the failure to fit the surplus production model successfully. Independently obtained average-size statistics are needed both to assess the resource under the assumption of north and south stocks and to investigate the validity of the assessment assuming a single Pacific-wide stock. Data on the drift gill-net fishery conducted off Japan need to be made available and incorporated into the analysis.

Sailfish

As indicated above, surplus production model assessment of the three presumed stocks of sailfish is not possible because of the broad nature of the FAO statistical areas and the reporting of sailfish and spearfish catches together in both the logbook and total catch statistics. However, the trend in the catch-rate statistics (Fig. 2) provides some information on the probable condition of one of the stocks. For index area 3, which is in the eastern tropical Pacific, catch rates were low during the beginning of the time series, increased drastically in 1966, suggesting that the resource was "discovered" commercially, then declined possibly because of excessive fishing pressure in prior years or a loss of interest by the fishing fleets. If the decline was due to fishing, then the fishery had a substantial effect on the density of the stock during the last 10 to 15 years of the time series, resulting in the stock now being at a much reduced level. The catch-rate trends for the other stocks do not show much variation over time and probably would not result in valid surplus production model estimates even if the data were available. If these sailfish stocks are to be assessed, fishery statistics specific to this species and these stocks must be obtained.

Shortbill Spearfish

As with sailfish, assessing the status of shortbill spearfish was not possible with the surplus production model because of the combined nature of the statistics and the relationship between the chosen index areas and the FAO statistical area (Fig. 1). The historical trend of catch rates for the hypothesized northern stock (area 1 in Fig. 2) shows fluctuating but increased abundance during the middle years of the time series, with the catch rate returning to previous levels by 1980. The catch rates are quite low throughout the time series, even by billfish standards, suggesting that the stock has not been seriously impacted by the tuna longline fishery and probably is in reasonably good shape. The Asian squid drift gill-net fishery, although operating mostly north of the index area for the northern stock of spearfish, may be of some concern.

For the assumed southern stocks, the trend in catch rates is more difficult to interpret (area 2 in Fig. 2) but may be related to changes in species targeting. Catch rates increased rapidly as the Japanese entered the south Pacific longline fishery for albacore and remained high until they began leaving the fishery (Skillman 1975), after which catch rate dropped precipitously. The real trend in abundance of this assumed stock is not clear from the available statistics.

Sailfish-Shortbill Spearfish Combined

Surplus production model assessment, using data for the entire Pacific, suggests that the combined fishery for sailfish and shortbill spearfish (Fig. 5) is still on the ascending limb of the production curve but closely approaching the MSY level of 10,000 to 12,000 t. This result implies that sailfish stocks are to some degree overharvested, since overharvesting of the spearfish is doubtful. Although the surplus production model fits the combined data reasonably well, investigating the 1965-1975 data, which deviate in a consistent fashion from the production model curve, might be informative.

Swordfish

The surplus production model assessment of this fishery indicates that the assumed, single Pacific-wide stock is being harvested below

MSY (Fig. 5). As indicated by the average weight statistics (Fig. 4) and the production curve, this fishery apparently has had three phases. First, a night-set longline fishery for small fish predominated from 1952 to 1961, and the fishery expanded, nearly reaching the estimated MSY. With the introduction, in 1962, of the day-set longline fishery, which harvests larger fish, catches exceeded the former production levels even as total effective effort declined through 1965. After that, fishing effort expanded, and the catches moved up the ascending limb of the production curve, but at a level comparable with those in the first period (1956-1961) for smaller fish.

Since deep longline gear has less effect on swordfish catches than any other billfish catches (Suzuki and Warashina unpub.), the production model for unadjusted data may be more appropriate. Since this choice leaves the data for the last few years out on the right limb of the production curve, the estimates of MSY and f_{opt} are reduced to about 18,000 t and 200 million hooks, respectively, and the fishery seems to be at about the point of MSY and f_{opt}. To improve this assessment, detailed information on fleet composition, fishing strategy, and fishing gear, including deep longline gear, must become available.

General

The status of most billfishes in the Pacific seems to have improved from 1975 to 1980, although the blue marlin is still being overharvested and swordfish and sailfish may be approaching that condition.

Japan is ceasing to release its data for use by the international community and is reducing the size of its tuna longline fleet. Korean and Taiwanese data have thus become more important for the assessment of billfish and tuna stocks. Consequently, the quality of Korean and Taiwanese tuna longline statistics must be improved, for example, by increasing fleet coverage and by accurately recording billfish catches. Because assessing some of the billfish stocks seems possible by employing the index area method, I propose that judicious selection of index areas would allow the international fishery community to continue monitoring the status of billfish stocks without compromising Japan's position in international and bilateral management negotiations.

Nations should strive to obtain separate statistics for blue and black marlins as well as for sailfish and shortbill spearfish. Coverage of coastal fisheries for swordfish could also be improved. Statistics from gill-net fisheries, whether billfishes are targeted or incidentally caught, and from purse-seine fisheries need to be made available.

The FAO fishery statistical areas for reporting total catches may be appropriate for coastal pelagic and demersal resources, but must be revised to facilitate assessment of offshore pelagic resources like billfishes and tunas. In the Pacific, area 77 is particularly in need of subdivision into Northern and Southern Hemisphere areas. Also the boundary between areas 61 and 71 in the western Pacific may be too far north for a reasonable division of north and south pelagic stocks.

For all billfish species, size data must be collected directly from landings, compiled, and published. Doing so will place the assessments on much sounder ground and allow evaluation of some of the unexpected trends seen for average weights calculated from total catch and logbook data, for example, for striped marlin.

Modeling of the potential effects of deep longline gear indicates that incorporating data on this development would improve the fit and accuracy of the production models. Hence, the distant-water tuna longline nations should be encouraged to modify their data collection procedures accordingly and to publish the resulting data.

Summary

Surplus production model assessments were completed, using geographic index areas for computation of indices of stock abundance, for Pacific stocks of blue marlin, swordfish, and sailfish-shortbill spearfish combined. No attempt was made to fit the model to black marlin data, nor to sailfish and spearfish separately, because of data problems, and no satisfactory fit could be obtained for striped marlin. Average weight statistics, computed from reported logbook numbers and FAO weight statistics, did not always follow expected trends, particularly for striped marlin for which the computed average weight increased throughout the history of the fishery. The effect of deep longline gear was simulated using assumed 25% and 50% reductions in the effective catch rates for billfishes. In general, the status of billfish stocks seems to have improved in the latter part of the time

series, from the late 1970s to 1980s, as estimated total effective effort declined, particularly under the assumption of declining overall gear effectiveness with the more widespread use of deep tuna longline gear.

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Robert A. Skillman received a B.S. in biology from Bradley University, an M.S. from Iowa State University (fisheries management), and a Ph.D. in 1968 from the University of California at Davis (zoology, specializing in resource management). Joining the Honolulu Laboratory, National Marine Fisheries Service, NOAA (then called the Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service), conducted research on pelagic species, e.g., stock assessment of South Pacific albacore, forecasting skipjack tuna catches in Hawaii, and age and growth of blue and striped marlins. In 1979-80, worked with FAO in the South China Sea Fisheries Development and Coordinating Programme to help establish what is now called the Indo-Pacific Tuna Development and Management Programme. Returning to the National Marine Fisheries Service in 1980, became leader of the Fishery Management Research Program, which is the primary interface with the Western Pacific Regional Fishery Management Council. In 1987, he returned to the area of pelagic species research with the creation of a research program directed at pelagic species under the Magnuson Fishery Conservation and Management Act, namely mahimahi (dolphin), wahoo, billfishes, and sharks.

8968

Stock Identification and Billfish Management

Robert A. Skillman

While economic and social evaluations of fisheries are today recognized as important elements in managing fisheries, determining the biological status of fish exposed to a fishery and to a management regime remains a basic and important element in management. For the status of a stock to be assessed, boundaries must be set. If the boundaries actually encompass more than one stock and management is carried out as if there were only one stock, the management scheme may perform satisfactorily on average for the two stocks. However, the more that population parameters, such as growth and mortality, differ among individual stocks, the more likely it is that the management regime will adversely impact one of the stocks. If the boundaries do not completely encompass a stock, then events external to the management area can significantly affect the stock.

This chapter reviews stock identification methods as they relate to fisheries management and, in particular, to billfish management. The stock concept, itself, will be discussed before reviewing the various methods used to study stock structure. Then, what is known about billfish stock structure will be reviewed, followed by recommendations regarding the most likely productive research strategies to follow for billfishes in the future.

The Stock Concept

Setting boundaries and identifying stocks is, in effect, determining what part of the total species population is going to be assessed and managed. Thus, the term stock or unit stock is used, ". . . to connote as well as circumscribe the basic grouping on which management needs to focus attention" (Kutkuhn 1981). This initial step in assessment has led to many reviews of the unit stock concept, with many authors proposing new or modified definitions. Providing a historical perspective might be appropriate at this time.

Fishery biologists first defined a stock in terms of the various tools employed in conducting an assessment. For example, Cushing (1968) said, ". . . a stock may be defined as a population in which the vital parameters of recruitment, growth, and mortality are homogeneous." In practice, fishery biologists frequently identified stocks based on where the fish were found as larvae, as adults in the fisheries, or while spawning, as well as by how the fish looked (meristics and morphometrics). Then, the existence of these putative stocks was evaluated by using estimates of vital (or population) parameters. With the development of population genetics, the fishery biologists' definition of a stock was viewed as vague and not quantitatively rigorous compared with the geneticists' definition of a population or a subpopulation. Thus, fishery biologists began incorporating genetic concepts, and new definitions were proposed. For example, ". . . a unit fish stock is one consisting of randomly interbreeding members whose genetic integrity persists whether they remain spatially and temporally isolated as a group, or whether they alternately segregate for breeding and otherwise mix freely with members of other unit stocks of the same species" (Kutkuhn 1981). Along with this definition came numerous attempts to identify stocks by using various genetic techniques.

The debate on the utility of genetic techniques in fisheries stock assessment and fisheries management continues today. One problem is whether a population determined to be genetically homogeneous meets the needs of fishery biologists to conduct stock assessments; namely, the unit stock must be homogeneous with respect to recruitment, growth, and mortality. A second problem is whether genetic techniques can resolve the structure of a large population inhabiting an extensive area having vague and changing environmental boundaries when biological (fishery) information suggests some degree of stock structuring. While all the evidence is certainly not in, the genetic and fishery biological definitions apparently coincide reasonably well for demersal species and stocks with well-defined physical or environmental boundaries. On the other hand, they apparently do not coincide well for species inhabiting, as adults or larvae, the pelagic ecosystem with poorly defined physical and environmental boundaries.

Stock Identification Methods

As indicated above, the study of population structure in fisheries consists of two basic approaches. The traditional biological approach consists of a number of alternative techniques for identifying stocks. These stocks meet the fishery biologists' stock asessment needs but may not be the same as genetic subpopulations. The newer genetic approach consists of a few but growing number of techniques for identifying subpopulations that may or may not be helpful for stock assessment and management purposes.

Biological

Distribution. Probably the first method employed was to examine the geographical distribution of fishery catches, which often consist of adults. Thus, this method has direct applicability to defining the boundaries of a fishery, and possibly the boundaries of management action, but it may not be satisfactory for determining the boundaries of a stock unless the distribution of fishing effort is extensive. For example, if the fishing effort is directed at the species being examined, it is not likely to occur beyond the region where the species is commercially or recreationally important. In such cases, stocks may be distributed more extensively than indicated. Compiling the distribution of catches by size classes may help substantiate the existence of putative stocks when recruitment can be shown to vary.

Determining the distribution of spawning sites may result in more reliable identification of stocks. The existence of geographically or temporally separate spawning sites, with no exchange of individuals among the sites, is necessary for genetic separation and could contribute to differences in vital parameters. The distribution of larvae and juveniles may also be used to identify stocks, particularly when the samples are collected independently from any fishery. Thus, using juveniles collected from the stomachs of commercially-landed predatory fishes should be done with care.

Population Parameters. Estimates of population parameters, such as growth, recruitment, and mortality, are used to separate stocks. In addition, they are commonly used to characterize putative stocks and evaluate whether their existence seems plausible; that is, whether the parameters are homogeneous over the range of the reputed stock. While demonstrating that parameter estimates are different among potentially separate stocks does not necessarily prove the existence of separate stocks, stock structuring is supported when geographical clumping or clinal variation of parameters occurs. Such results are consistent with a lack of genetic mixing (subpopulation formation) and a lack of exchange of fish among fishing grounds or mixing of individuals in nursery areas (stock formation) because separation, from either perspective, could lead to different population parameters. Given the poor ability to estimate mortality even for well-studied stocks, however, estimates of billfish mortality are not likely to provide as much information as growth estimates. On the technical side, comparison of the growth estimates is complicated because the commonly used von Bertalanffy growth parameters, maximum size (L_{inf}) and rate of approaching that maximum (k), are correlated. Simple cluster analysis conducted by plotting L_{inf} versus k for samples from different areas has proven productive in the identification of stocks. Other population parameters (e.g., the age at first maturity and gonadal index) are also used. Age at first maturity is strongly affected by stock size, which is, in turn, affected by the size of the fishery. Gonadal development is seasonal but may differ among stocks.

Parasites. Using the occurrence of fish parasites as a means of studying stock structure is based on the concept that parasites are naturally occurring "tags"; that is, the incidence of parasitic species varies geographically and these natural tags are not lost. The method is not applied frequently to large pelagic species for a number of reasons. Fishery biologists recognize that parasitology is not a tool in the sense that morphometric and multivariate statistical methods are, but is an additional level of biological complexity requiring research itself. This complexity involves the identification of relatively bizarre animals; use of different sampling, preservation, and preparation techniques; and, most importantly, familiarity with a different set of life-history strategies involving host-parasite relationships. Parasitologists have tended to work more in freshwater and coastal marine habitats where fish stock sizes and parasite-to-host linkages are more amenable to reseach. Consequently, the life histories of parasites occurring on large pelagic species and the effect of environmental changes on infestation are not well known, and interpretation of results has been open to question. Research is needed on the possibility of tag loss (selective or differential loss of parasitic species or parasite size classes) with movement of fish into areas having different environments, and then reinfestation by other parasitic species. Also, application of the method to date has assumed that each natural tag (each parasitic species) is made up of one population, but I see no reason why they could not be divided into subpopulations as well. Nonetheless, such studies can provide a fishery-independent determination of stock structure, and additional long-term work on the basic biology of pelagic fish parasites is likely to improve the utility of the method as a stock identification tool.

Tagging. Tagging fish for the study of stock structure is very popular because it provides direct, if not irrefutable, evidence of fish movement and the lack of stock separation. Movement is the mechanism for exchange of individuals and the mixing of genetic products. However, the method has several problems, and care must be taken in analyzing the results (Hilborn and Sibert 1988). First, the method is expensive if large numbers of tagged fish are to be released, and this is certainly desirable if not a requirement with the large populations that exist for billfishes and other pelagic species. Also, a great deal of international promotion and cooperation are required to conduct such experiments successfully. Second, results are meaningful only if fisheries exist that have the potential of recapturing the tagged fish. Third, fishing effort statistics from these fisheries are required for quantitative evaluations of the recaptures. Fourth, without additional information about the biology of the fish and such specifics as the size and maturity of the fish when released and retaken, recaptures may indicate movement but provide little information on stock structuring.

Morphometrics and Meristics

Fish exhibit greater observable (phenotypic) variation than other vertebrates, apparently because they are poikilothermic (cold-blooded) and have a capacity for indeterminate growth (e.g., Allendorf et al 1987). Thus, early workers were able to recognize stocks on the basis of appearance, and later workers built on this by analyzing measured characters (morphometrics) or analyzing counted characters (meristics). With the development of analytical tools in the fields of taxonomy and statistics, this approach flourished and provided a means for rigorously identifying stocks. However, morphometric and meristic characters were shown to be strongly influenced by the environment, and their use fell into disfavor with the development of electrophoresis for studying population genetics. Experience has shown that stocks identified by using morphometrics or meristics are in general agreement with subpopulations identified genetically (e.g., see Ihssen et al 1981). However, a greater degree of stock structuring is often found by using morphometric and meristic methods than by using genetic procedures, because of the superior power of the statistical tests associated with the former methods and the use of environmentally influenced characters.

Thus, among many biologists, morphometric and meristic methods are still viable means of investigating stock structuring. With the development of new techniques for studying shape, the statistical power of the methods has increased even more. Truss analysis (e.g., see Winans 1987) makes use of recently developed powerful multivariate analysis techniques. Showing great promise is the use of planar shape analysis, first used in the study of the evolution of ostracods (e.g., see Benson 1967) and recently making its way into fisheries (Bird et al 1986). This method is based on pattern recognition techniques using mathematical tools such as Fourier analysis and discriminant analysis. The collection of data for analysis using the truss and planar shape methods can be performed on microcomputer-based image processing systems, thus reducing the cost of collecting data in the field.

Genetics

The following historical perspective is drawn in part from Utter et al (1987). Although great strides in the inheritance of observable characters have been made from the time of the pioneering work of Mendel (1866) up to the 1930s, this work was not transferable to fish because of the magnitude of environmental influences on their observable characters. About this time, the inheritance of blood groups had been resolved, and attempts were made later to use the technique on tunas (Cushing 1956, Sprague et al 1963, Fujino 1970). This technique was unproductive because of the fragility of fish erythrocytes and problems in making and preserving the discriminating antisera. Lundstrom (1987) indicates that the use of monoclonal antibodies shows promise, but other genetic procedures probably show more potential for success with billfishes.

The determination of the structure of the DNA molecule by Watson and Crick (1953) led quickly to the determination of the relationship between genes and intracellular, enzymatic proteins, called isoenzymes or isozymes for short. By 1955, electrophoretic techniques were developed that allowed easy examination of the variation (polymorphism) of these proteins and, thereby, the genes that make them. Thus was born the most powerful and productive technique to date for studying population genetics, dominating since the mid-1960s. Examples even in the fisheries literature are too numerous to mention. A serious problem with the technique is that separation of stocks depends on statistically testing of what are called the Castle-Hardy-Weinberg gene proportions. This test is statistically weak and, with the typical genotypic ratios involved, requires large sample sizes to obtain meaningful results. After many years of work on skipjack tuna *(Katsuwonus pelamis)* in the Pacific Ocean (Fujino and Kang 1968, Argue et al 1986), some degree of population structuring is indicated, but distinct subpopulations have not been resolved. Grant et al (1987) state that marine fish, in general, exhibit little genetic population structuring because of the passive dispersal of larvae and active movement of adults (Ryman et al 1984; Shaklee 1984). Given the life history of most billfishes, electrophoretic study of isozyme variability is not likely to be very productive.

Recently, two additional DNA-based techniques have been developed. As the name suggests, DNA sequence determination involves the resolution of genes directly on the DNA molecule, which is located in the cell nucleus. The method is sufficiently sensitive that relatedness of progeny and ancestors of a generation or two can be detected; beyond this, variability becomes so great that all individuals appear to be different (Wetton et al 1987). Thus, the name "DNA fingerprinting" has been used to describe this method. It is not likely to be of much benefit for the study of billfish stock structuring, although it may be the genetic "marker" so long sought for hatchery-reared fish released into the wild.

The second technique involves the analysis of DNA occurring in mitochondria located in the cell cytoplasm. Because mitochondrial DNA (mtDNA) is maternally inherited, each individual has an exact copy (except for rare mutations) of the mtDNA genotype from its mother. Therefore, the operational taxonomic unit is the individual rather than the population, as with nuclear gene analytical techniques such as electrophoresis. Thus, in practical terms, the statistical requirements are quite different, and sample sizes can be substantially less than with electrophoretic work (Ferris and Berg 1987). For example, reported sample lot sizes per species have varied from 1 to 12 (Avise et al 1979, Berg and Ferris 1984, Graves et al 1984, Wilson et al 1985, 1987) with species totals in 2 studies reaching 36 (Avise et al 1979) and 87 (Lansman et al 1981). This contrasts with sample lot sizes of 50 to 100 (Fujino and Kang 1968) or even 200 (IATTC 1978) and total sample sizes in the thousands for electrophoretic studies of fish. Although the technique apparently holds great promise for resolving stock structuring (Avise et al 1979), little experience has been gained with pelagic species. Avise (1987) could not find any evidence of stock structuring in the American eel *(Anguilla rostrata)* which spawns in the pelagic environment, whereas stock structuring was evident for several demersal or estuarine species. Graves et al (1984) did not find any difference between Atlantic and Pacific samples of skipjack tuna; however, the specimens were frozen, which considerably reduces the amount of mtDNA recovered for analysis (Lansman et al 1981; Ferris and Berg 1987).

Billfish Stock Structure

In the following sections, information on the stock structure of billfishes is summarized from a variety of sources. Papers presented at the first billfish symposium in 1972 (Shomura and

Williams 1974) discuss, for Atlantic, Indian, and Pacific oceans, the distribution of adults based on tuna longline catches, the distribution of larvae and ostensible spawning areas based on research data, and results from tagging. For the Atlantic Ocean, I am not aware of any single source summarizing information on billfish stock structure, so I have used the way billfish stocks are assessed and reported in the biennial reports of the International Commission for the Conservation of Atlantic Tunas (ICCAT) as an indication of the state of knowledge (e.g., see ICCAT 1987). For the Indian Ocean, participants at a 1979 tuna and billfish stock assessment workshop summarized the state of knowledge for billfish stock structure (FAO 1980). Likewise, for the Pacific Ocean, participants at the 1977 billfish stock assessment workshop (Shomura 1980) summarized what was known about the stock structure of billfishes as a prerequisite to assessing the status of the presumed stocks.

Atlantic Ocean

Among the several billfishes occurring in the Atlantic Ocean, the ICCAT biennial reports contain material on separate stocks only for sailfish *(Istiophorus platypterus)*, namely eastern and western stocks. The basis for this separation seems to be the distribution of longline catches and tagging results (Mather, Tabb, Mason, and Clark 1974). While tagging results support the existence of separate northern and southern stocks of the Atlantic blue marlin *(Makaira nigricans;* Mather, Mason, and Clark 1974), the ICCAT reports contain discussions of stock assessment results for the entire Atlantic Ocean but present figures showing surplus production models for separate stocks. White marlin *(Tetrapturus albidus)* assessments are presented for one Atlantic-wide stock. For swordfish *(Xiphias gladius)*, researchers (ICCAT 1987) now believe that separate eastern and western stocks exist, as well as a separate Mediterranean stock, based on longline catch distributions, tagging results, and the distribution of spawning activities and larvae.

Indian Ocean

Information on the stock structure of five billfishes is available for the Indian Ocean (FAO 1980). The distribution of longline catches and information on spawning suggest that there is a single stock of Indo-Pacific blue marlin *(M. mazara)* in the Indian Ocean. Similar kinds of data for striped marlin *(T. audax)*, swordfish, sailfish, and black marlin *(M. indica)* suggest multiple stocks. In addition, the workshop participants (FAO 1980) believed that movement of the latter species could occur between the Pacific and Indian Oceans although no tag recaptures had been made to support the contention.

Pacific Ocean

For the Pacific Ocean, stock structure information is available for six billfishes (Shomura and Williams 1974, Shomura 1980). Based on the distribution of tuna longline catches, tagging returns, and the distribution of spawning, the Indo-Pacific blue marlin is believed to consist of a single Pacific-wide stock (Shomura 1980), whereas the other billfishes exhibit some evidence of stock structuring. In an electrophoretic survey of blue marlin captured in Hawaii, sufficient polymorphism to conduct a population genetic study was found (Shaklee et al 1983). The only suggestion of population structuring (mixing of subpopulations) in this small sample collected at one site in 1 month, however, was a deficiency of heterozygotes for one of seven polymorphic gene systems surveyed. For black marlin, participants at the 1977 stock assessment workshop (Shomura 1980) indicated that separate eastern Pacific and two western Pacific stocks probably exist. Skillman (1989) assumed one Pacific-wide stock centered off Australia, based on the distribution of tuna longline catches. Nakamura (1983) indicates two spawning areas, one off Australia and a second in the north Pacific between the Caroline and Marshall Islands. Northern and southern stocks of striped marlin may exist, but the evidence is contradictory or inconclusive. For striped marlin, the area of high tuna longline catches in the eastern tropical Pacific appears to join or merge seasonally in many years with high catch areas in the middle latitudes of both the north and south Pacific. In contrast, the annual distribution of spawning stretches from comparable northern and southern central Pacific areas across the Equator in the western tropical Pacific (Nakamura 1983). Swordfish population is generally believed to consist of a single Pacific-wide stock, but may consist of separate stocks in the northwest, southwest, and eastern Pacific. Spawning grounds are located in warm, tropical waters in the western and central Pacific (Nakamura 1983). Sailfish are believed to be divided into eastern and western stocks based on tuna longline catch rates and distribution of spawning sites. Distribution of tuna longline catches suggests separate northern and southern stocks of shortbill spearfish *(T. angustirostris)*, and the distribution of spawning activity supports this conclusion.

Recommendations

The following research recommendations would, in my opinion, most likely contribute to our understanding of the stock structure of billfishes.

1. Tag-and-release programs, particularly for young fish, should be continued and extended to other tournaments and fisheries. Recaptures provide valuable information on movement and the relationship among fisheries, information not easily gotten by any other means. Although the number of billfish that could be released from most fisheries is small, and indeed probably smaller than desirable for estimating such parameters as fishing mortality, growth rate, and rate of exchange between fisheries, qualitative information on movement is still useful. Returning viable billfish to the sea without tagging them, or retaining all nontrophy or nonpoint-contributing billfish for tournaments, is, in effect, throwing away a valuable research opportunity. Support of tagging operations is particularly amenable to cooperative arrangements among national fishery agencies and recreational interests and, indeed, could provide the basis for further cooperation.
2. More effort should be expended on shape analysis, especially the newer truss and planar shape methods, but possibly on traditional morphometric and meristic methods as well. Although the newer methods require or would benefit from access to microcomputer-based image processing equipment and some specialized computer software (though not very sophisticated or costly), the traditional methods can be used by small fisheries offices with measuring devices, a microcomputer, and standard statistical software. Such studies would benefit from intergovernmental cooperation and, of course, collaboration with fishermen, tournament organizers, and fish processors.
3. Studies should be conducted to estimate vital parameters, such as growth, age at first maturity, recruitment, and mortality, to ensure that valid stocks are identified and that models used to assess the status of stocks are applied correctly.
4. Billfish larval surveys should be designed and implemented. Results from ichthyoplankton tows, taken by different kinds of gear, at different depths, in different seasons, and, for the most part, without any experimental design (along with charts of the distribution of billfish catches by tuna longline gear), have been the most commonly used means of identifying stocks. Enough is now known, however, about the location of spawning grounds and seasonal occurrence of spawning for most billfishes, to formulate testable hypotheses about their stock structure. Because of the large areas involved, such experimentation would benefit from international collaboration among national fisheries agencies and universities.
5. Selected genetic studies using mtDNA or electrophoresis should be continued but not on a large scale. I suggest that selecting species such as sailfish, generally believed to consist of multiple stocks, would be more productive than choosing a species thought to consist of one panmictic stock. Also, regarding mtDNA analysis, the development of standard tissue collection and preservation procedures for situations where the samples cannot be immediately processed would benefit billfish research.

Summary

The identification of separate biological units or stocks is required for determining the status of the resources and for conserving them via fisheries management. A number of biologically based methods for separating stocks are available; using such methods on billfishes is likely to be more productive than using population genetic methods. The stock structures of billfishes are, in general, poorly known. The largest billfishes, blue and black marlins, appear to consist of single ocean-wide stocks, while there is some evidence for east and west or north and south stocks of the smaller striped marlin and swordfish. Evidence for multiple stocks for the smallest species (spearfish and sailfish) is stronger.

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8969

ANALYSIS OF THE PATTERNS OF DISTRIBUTION OF ZOOPLANKTON AGGREGATIONS FROM AN ACOUSTIC DOPPLER CURRENT PROFILER

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ABSTRACT

A test set of data of volume reverberation, measured from the R/V *New Horizon*, nominally from 12–240-m depth in 4-m intervals, was taken in April 1988 using a 307-kHz acoustic Doppler current profiler (ADCP). A vertical profile was produced each minute for three days over the San Diego Trough off southern California. The results show kilometer-scale zooplankton aggregations with somewhat larger gaps between them. The area profiles had about 10% coverage of zooplankton aggregations. Aggregation target strengths were usually stronger during the morning and evening migrations. Migration rates were of the order of 5–8 cm s^{-1} during ascent and 3–4 cm s^{-1} during descent. Zooplankton aggregations were of horizontal dimensions intermediate between fish schools and groups of schools.

RESUMEN

En abril de 1988, a bordo del buque de investigación *New Horizon*, se colectó una serie de datos de volumen de reverberación, haciendo uso de un aparato de 307 kHz para perfilar la corriente doppler acústica (PCDA), abarcando una profundidad de 12 a 240 m en intervalos de 12 m. Se midió un perfil vertical cada 1 minuto, por un período de 3 días, en la Depresión de San Diego, frente al sur de California. Los resultados indican agregaciones de zooplancton en escalas de kilómetros, con espacios algo más grandes entre las mismas. Aproximadamente 10% del área de los perfiles presentaron agregaciones de zooplancton. Las fuerzas de blanco de agregaciones fueron, en general, más fuertes durante las migraciones matutinas y vespertinas. Las tasas de migración fueron del orden de los 5 a 8 cm seg^{-1} durante el ascenso y de los 3 a 4 cm seg^{-1} durante el descenso. Las dimensiones horizontales de las agregaciones de zooplankton fueron intermedias entre cardúmenes de peces y grupos de cardúmenes.

INTRODUCTION

Distributional patterns in the pelagic habitat are known to exist at several time and space scales (Haury et al. 1978; Greenlaw and Pearcy 1985). Some spatial scales have been evaluated for some planktivorous pelagic schooling fish (Graves 1977; Fiedler 1978; Smith 1978b), zooplankton (Star and Mullin 1981; Haury and Wiebe 1982; Pieper and Holliday 1984), and mesopelagic micronekton (Greenlaw and Pearcy 1985). Two aspects of plankton sampling that must take account of these scales are (1) estimation of the abundance of a species and (2) an understanding of the interactions between planktonic organisms and their immediate environment, principal predators, competitors, and food organisms.

Vertical and horizontal integration can increase the precision of estimates of abundance of "patchy" organisms in the plankton sample (Wiebe 1972). The integrated sample, however, may underestimate the local density of an organism by sampling volumes at inappropriate depths, or may include species with which the target species never interacts. Resolving the patchy dispersion of prey within a fluid volume is important for estimating attack rates by predators (Ohman 1988a).

The space scales relevant to a particular population or process are invisible in the pelagic habitat. Pilot sampling studies are necessary to help formulate and constrain the questions to be answered (Andrews and Mapstone 1987). Acoustic methods can be useful for such preliminary surveys, as a means to obtain rapid, broad coverage, and as a tool to direct other, invasive sampling methods. Acoustic methods are not generally useful for identifying organisms or precisely estimating their biomass. A continuous acoustic record can be used to delineate spatial scales that must be encompassed or resolved (Holliday 1985).

Studies of the scale and intensity of fish schools have been used to design and interpret surveys of northern anchovy eggs (Smith 1970; Hewitt et al. 1976; Graves 1977; Fiedler 1978; Smith 1978a,b, 1981; Smith and Hewitt 1985a,b). Two major find-

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ings of this work that depended on acoustic technology are that (1) on the small scale, within a school, the biomass of fish is on the order of 15,000 grams per square meter of horizontal surface, and their consumption of plankton would be approximately 750 grams per square meter of fish school horizontal surface per day; and (2) the fish schools of tens of meters in diameter are assembled in concentrations of shoal groups extending for tens of kilometers. We do not know the rules of assembly of shoal groups: one mechanism could be that schools' swimming speeds decrease and turning behavior increases when the school is in the upper ranges of plankton biomass. The lower ranges of plankton biomass could be a temporary result of foraging groups of schooled fish (Koslow 1981).

In addition to the spatial complexity of the pelagic habitat at several horizontal scales, rapid changes in the vertical distribution of organisms at dawn and dusk are well known (Enright 1977; Pieper and Bargo 1980). The impact of these migrators on the distribution pattern of their prey must be added to the direct effects of diel vertical migration on the distribution of plankton. Initial time and space scale information from acoustical methods may be useful in designing the most effective direct sampling procedures for studies of fine-scale processes and of geographic-scale population abundance.

Acoustic profiles may be used to estimate the scale and intensity of patchiness and to help specify the number, size, and placement of samples. The primary sampling design questions to be asked in pelagic studies are:

> How many samples are needed?
>
> How big should the sample units be?
>
> At what separation distance can adjacent sample units be said to be effectively independent?
>
> Over what spatial and temporal scales are processes operating?
>
> What are limits of the temporal and spatial scales to be used for such studies?

It is the purpose of this study to report the qualitative spatial analysis from several days of continuous acoustical sampling. From these records, we will summarize the incidence of biological aggregations, their spatial dimensions, the dimensions of the spaces between aggregations, the depth distribution of aggregations, and the rates of change in depth.

METHODS

The pilot study was conducted in a 5 by 15-n. mi. area oriented SE NW about 25 n. mi. west northwest of San Diego (figure 1). The equipment used included a 307-kHz acoustic Doppler current profiler (ADCP)[1], a multiple opening-closing net, and environmental sensing system (MOCNESS, Wiebe et al. [1985]), and standard hydrographic bottle casts. It is important to note that the ADCP had not been calibrated in the amplitude domain and that the effect of methods of conditioning the amplitude signal have not been studied. The Sea-Bird Electronics temperature sensor on the MOCNESS frame was calibrated against deep-sea reversing thermometers. Chlorophyll *a* and pheopigments retained on Gelman GF/F filters were extracted in refrigerated acetone and analyzed on a Turner Designs Model 10 fluorometer. Dissolved oxygen was determined by the Carpenter (1965) modification of the Winkler titration method. The MOCNESS (20 nets, 1-m^2 effective mouth area, 333-μm mesh) was towed at about 50–75 cm s^{-1}. A nighttime profile was made from 500 m to the surface in approximately 50-m intervals between 0131 and 0401 on April 6, 1988. A comparable daytime profile was made from 1330 to 1510 on April 6. Volume filtered per haul averaged 354 m^3 (range 156–927 m^3). Samples were preserved in 10% Formalin buffered with sodium borate. Select copepod species were enumerated after subsampling with a Stempel pipette; when organisms were rare the entire sample was counted.

Acoustical Methods

The primary function of the ADCP is to sense current direction and speed as a function of depth. It accomplishes this by detecting the Doppler frequency shift of backscattered sound from planktonic organisms, particles, and small-scale discontinuities in the water column. This frequency shift is proportional to the relative velocity between the backscattering source and the transducer. The change in frequency is measured by four transducers. Unlike echo sounders having the transducer aimed downward, or sonars (*so*nically determined *a*zimuth and *r*ange) having the transducer directed laterally at any angle with reference to the bow, the four ADCP transducers are oriented at 30° from the vertical: approximately forward, aft, right abeam, and left abeam (figure 2). This means that the axes of the complementary beams are as far apart as the depth ($2 \times \sin(30°) = 1$) below the transducer. In

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[1] Manufactured by RDI Inc. San Diego. (Mention of manufacturer does not imply endorsement by the U.S. government or the University of California). A more complete technical description is available in a manual from the manufacturer. See also Flagg and Smith (1989).

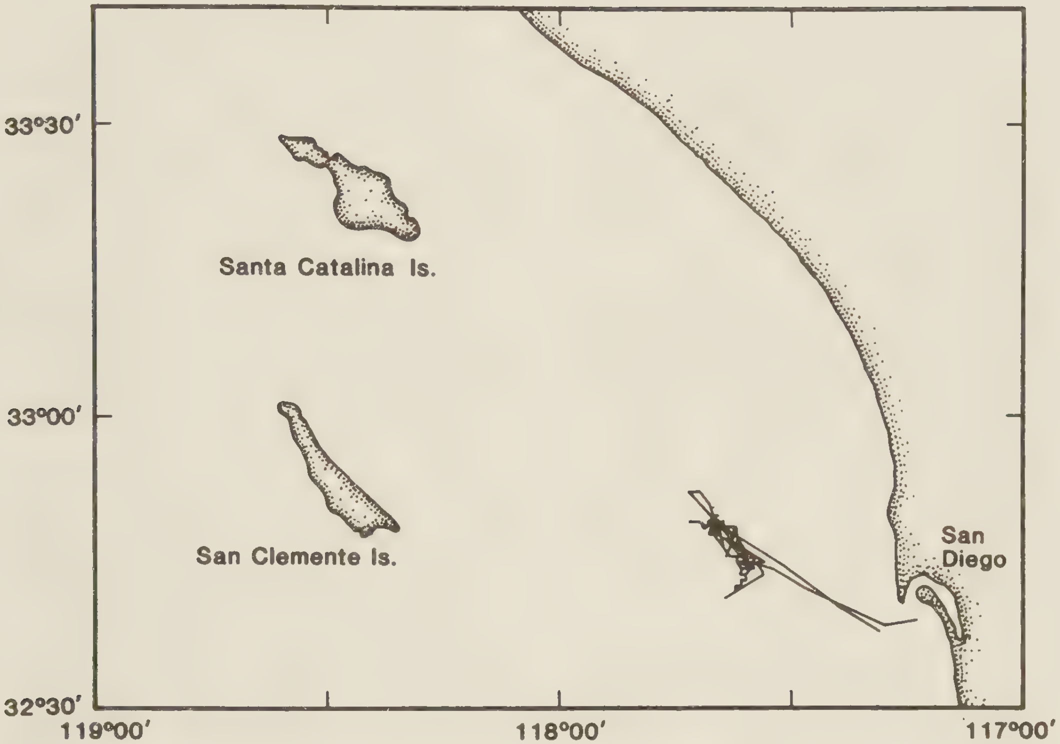

Figure 1. Track of R/V *New Horizon* during ZB1 cruise. Data were collected during the entire cruise. See figure 8.

this report we analyze the information content of the echo amplitudes, rather than their frequencies.

The speed of sound in water is approximately 1500 meters per second. Therefore a sound oscillation of 300,000 cycles per second (Hz) has a wavelength of 5 mm; in general, insonified objects much larger than 5 mm scatter sound more efficiently than objects equal to or smaller than 5 mm (Holliday 1980). The proportion of the sound transmitted through, reflected from, and scattered around the object is influenced by small contrasts between the compressibility and density of water and these features of the object. For example, an organism with a bony skeleton, scaly integument, and air bladder returns much more sound than an organism which is primarily protoplasm. Similarly, organisms that are aggregated into patches or layers return more scattered sound per unit of local volume than the same organisms would if distributed evenly throughout a larger volume.

The probability that the acoustic pulse will encounter a target increases with depth because the widths of each acoustic beam increase with depth (figure 2). The probability of detection of a given target decreases with depth because the sensitivity of the receiver is fixed but the sound available for reflecting or scattering is decreasing as the inverse square of the range. In addition, there is a frequency-specific attenuation of sound in water, with more sound lost as a function of range in the higher frequencies. To use the ADCP as an acoustic sampling system, we must be able to define the conditions of encounter and the probability of detection. Targets smaller than 240 m cannot be resolved at the deepest depths because of the transducer beam geometry.

The ADCP used in the April cruise operated at 307.2 kHz. The transducer installation on the R/V *New Horizon* was 4 m deep (the draft of the ship), and the outgoing pulse was set at 4-m length (2.7

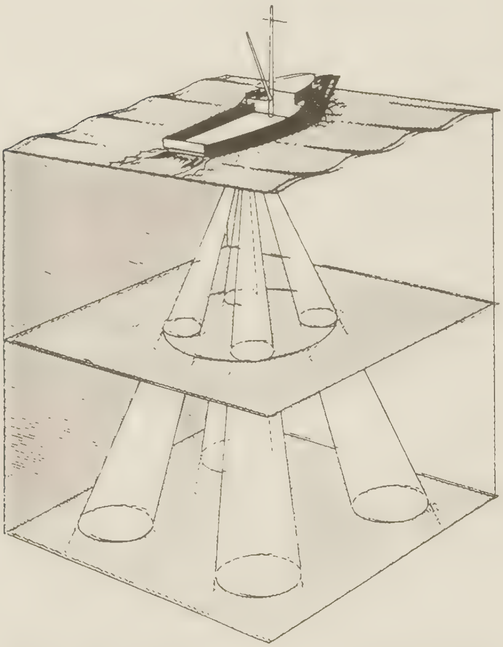

Figure 2. Diagram of the insonification pattern of an acoustic Doppler current profiler (RDI Inc. manual). Contrary to the diagram, the actual orientation of beams is 2 fore and aft and 2 left and right.

msec). Since the near-field return data (4 m) were not collected, the first data on the water column acoustic backscatter were obtained from a depth of about 12 m (figure 3). All graphical zero depths actually refer to 12 m. For each pulse, the amplitude of the return and the estimated velocity of the layer were stored in 60 depth "bins," each representing 4 m. Following nearly a minute of pulses at 1-second intervals, the ensemble average of each bin was calculated, and this average was stored as a compact binary record on a floppy disk. The ensemble averages of the previous profile were also displayed at the operator's console as the next ensemble was being taken (figure 3). Two of the four vertical profiles stored each minute are the velocities of the 4-m layers relative to ship's motion, as a function of depth. One of these profiles displays current speed at right angles to the ship's motion, and the other in the direction of the ship's motion.

There are two accessory profiles. One is the automatic gain control (AGC), which indicates echo amplitude with depth, and the second is the "percent good" value, which indicates the percentage of pings exceeding the signal-to-noise threshold. Note in figure 3A that the AGC is primarily a decreasing function of depth and that "percent good" remains above 90% in the first 60 m below the ship, declines to 75% by 180 m, to 25% by 210 m, and to less than

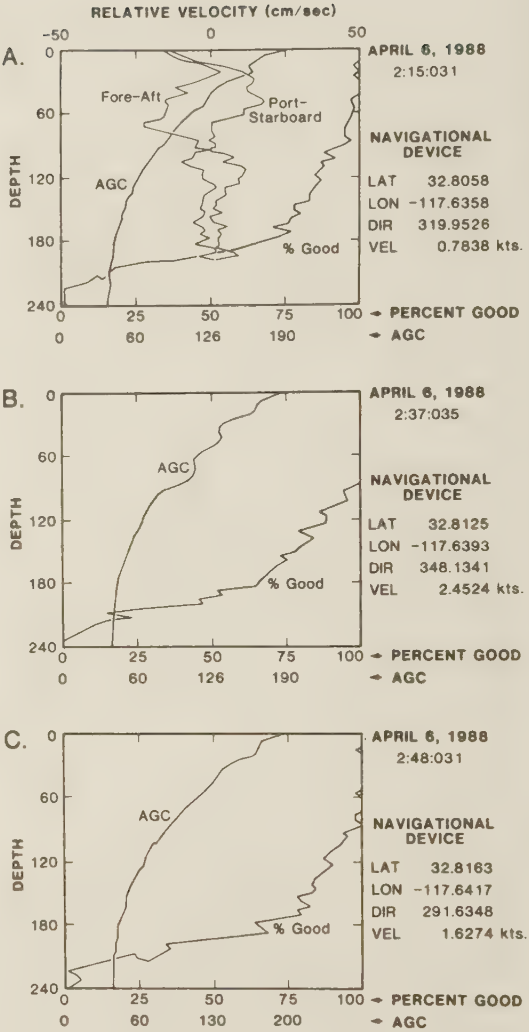

Figure 3. Specimen profiles. *A*, The velocity curves extend from 0 to 200 m and represent the water-layer motion after the effect of ship's motion in these planes has been removed. One velocity curve is the port-starboard velocity; the other is the fore-aft velocity. The curve labelled AGC is the automatic gain control. The last curve is the "percent good" value expressed as the percentage of pings in the ensemble that were analyzed for frequency at each 4-m depth interval. When this value drops below 25%, the analysis of velocities stops. *B*, Profile taken 22 minutes later, showing the effect of targets on the AGC profile. Velocity curves have been removed for clarity. *C*, Profile taken after the targets had passed.

A.

DEPTH (m)	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68	72	76	80	84	88	92	96	100	104	108	112	116	120	124	128	132	136	140	144	148
0215 ←	190	177	169	162	159	163	154	144	135	130	126	125	124	120	112	107	104	101	98	92	91	90	85	81	77	75	72	71	69	65	62	60	61	59	57
	190	175	166	164	159	164	155	143	136	130	126	125	123	120	113	108	103	102	97	94	91	89	86	81	79	75	72	71	68	67	64	62	60	61	57
	191	176	166	162	161	163	154	143	136	130	128	124	123	118	113	108	103	100	96	94	90	90	86	82	79	76	75	70	68	64	62	62	60	60	57
	189	176	167	162	161	164	154	142	135	132	128	124	121	119	112	108	101	101	96	95	92	90	86	82	77	76	73	70	68	66	64	63	62	60	57
	187	175	167	164	160	163	153	143	135	130	129	125	122	118	113	107	103	101	95	93	90	91	86	81	77	76	74	71	68	66	62	63	61	60	57
	185	176	168	163	159	164	152	142	135	131	128	125	122	118	113	107	101	99	96	94	92	90	86	81	78	75	73	70	68	66	62	62	61	59	56
	184	176	169	166	161	164	152	142	134	131	130	124	122	119	112	106	101	99	95	94	90	91	85	83	77	76	74	70	69	66	64	62	61	59	58
	184	175	167	165	161	163	153	141	135	132	129	123	122	119	111	105	103	98	97	93	91	89	84	82	76	77	74	70	68	67	63	62	61	60	59
	183	174	167	165	160	164	154	142	133	130	129	125	120	118	112	107	102	99	96	93	91	90	86	80	78	75	74	71	68	67	62	62	61	60	57
	183	175	169	165	160	163	153	140	135	130	130	126	121	118	112	107	102	99	97	94	91	90	85	81	77	74	73	70	70	67	62	62	61	59	56
	183	174	168	164	161	163	149	140	133	131	127	124	121	118	113	107	104	100	98	96	91	91	85	81	77	76	75	71	69	67	64	63	60	61	58
	184	176	169	163	163	163	150	139	134	131	129	125	121	117	112	106	103	100	97	95	92	90	85	80	77	76	73	71	70	67	66	63	62	61	58
	182	175	169	164	163	165	150	140	133	130	129	124	121	118	112	106	102	101	98	94	92	89	85	79	79	76	73	70	70	67	63	62	61	60	57
	184	175	169	164	162	165	153	140	131	130	129	125	121	118	111	107	102	101	99	96	92	89	84	80	79	77	73	71	71	67	65	64	62	59	56
	185	175	168	164	164	163	149	140	134	132	128	124	123	118	112	107	104	100	100	96	91	90	86	79	78	76	74	71	71	68	66	64	60	59	56
	185	174	169	164	164	161	149	141	136	131	129	124	122	118	112	109	104	102	102	98	93	92	86	81	77	77	73	72	70	69	65	64	60	59	57
	185	175	168	165	163	164	151	141	134	131	128	125	122	119	114	108	106	102	103	101	96	91	87	80	78	76	74	72	69	68	67	63	61	60	57
	185	174	168	164	161	164	151	140	133	130	129	125	121	120	115	110	106	104	105	103	98	93	88	81	77	77	74	71	69	68	67	65	61	60.	57
	185	175	168	165	161	164	154	141	135	130	129	127	122	122	115	111	108	106	108	106	101	95	89	82	79	76	75	71	69	69	67	65	62	60	57
	186	176	170	163	161	163	152	142	135	129	130	129	124	121	116	112	106	107	108	108	104	97	90	83	77	78	75	71	70	69	69	66	62	61	59
	186	174	170	165	163	162	151	140	134	129	133	130	126	122	117	112	110	108	108	109	105	100	91	85	79	77	75	71	70	67	67	66	63	60	59
	185	175	170	164	164	160	148	139	134	133	137	133	127	122	118	112	112	109	111	110	106	100	92	85	80	77	74	72	71	69	67	65	63	61	59
0237 ←	186	175	169	166	165	159	147	139	134	133	139	136	129	123	118	113	111	110	112	111	109	102	93	83	78	76	74	72	71	70	68	65	64	62	59
	187	176	168	165	166	160	146	138	134	133	137	135	131	123	118	114	111	113	114	112	110	103	94	84	80	78	74	71	71	69	68	67	64	61	60
	186	174	168	165	164	162	149	139	133	131	136	138	131	125	118	112	113	114	115	113	108	103	94	85	81	78	75	71	70	69	69	66	64	62	58
	186	175	169	165	164	163	149	138	134	130	134	136	130	125	120	115	112	115	115	111	108	101	94	87	80	77	75	72	70	68	68	65	63	62	61
	186	176	169	166	164	163	149	140	134	131	134	133	129	124	120	118	114	113	115	111	108	101	94	85	82	78	74	72	70	70	69	66	63	61	59
	187	176	169	167	164	161	147	138	134	129	133	133	128	123	119	116	114	110	111	109	105	100	94	87	81	78	74	72	71	69	67	65	64	60	58
	186	175	170	166	165	159	146	139	133	130	131	130	127	124	118	116	111	111	111	106	103	97	92	86	81	77	72	72	70	69	67	65	62	62	59
	185	175	170	165	165	159	147	138	133	129	131	128	126	122	119	113	110	109	109	104	100	96	90	83	80	77	73	71	69	67	66	65	63	61	60
	187	175	169	166	166	160	147	142	134	129	130	129	126	123	116	113	110	106	107	103	97	94	88	82	82	76	73	72	71	69	66	64	62	61	58
	186	176	169	166	165	161	146	141	136	130	130	129	126	121	116	111	108	106	104	99	96	92	87	84	80	76	72	71	72	70	67	65	62	62	59
	188	175	168	167	165	163	149	142	134	131	130	128	125	123	116	112	107	104	103	97	95	92	88	84	81	78	73	72	71	70	68	65	62	59	59
0248	187	176	167	165	165	163	150	143	136	132	129	129	124	121	117	111	108	103	101	96	93	92	87	83	80	78	73	72	71	68	68	65	63	61	59
	184	169	170	166	168	166	153	143	138	135	130	127	125	124	122	116	111	107	102	97	93	89	83	81	78	75	73	71	70	69	65	66	65	63	61
N ←	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240	240
MEAN ←	188	175	167	163	162	162	153	143	137	133	131	127	123	119	115	110	106	103	99	96	93	91	86	82	79	77	74	71	69	67	66	65	63	62	60
STANDARD DEVIATION ←	2	3	2	3	5	4	4	3	2	2	3	3	3	2	2	3	3	3	4	4	4	3	3	2	2	2	2	1	2	2	2	2	2	2	2

B.

DEPTH (m)	12	16	20	24	28	32	36	40	44	48	52	56	60	64	68	72	76	80	84	88	92	96	100	104	108	112	116	120	124	128	132	136	140	144	148
0215 ←	1	1	1	0	0	0	0	0	-1	-1	-2	-1	0	0	-1	-1	-1	0	0	-1	-1	0	0	-1	-1	-1	-1	0	0	-1	-2	-3	-1	-1	-1
	1	0	-1	0	0	1	0	0	0	-1	-2	-1	0	0	-1	-1	-1	0	-1	-1	-1	0	0	-1	0	-1	-1	0	-1	0	-1	-2	-2	0	-1
	1	0	-1	0	0	0	0	0	0	-1	-1	-1	0	0	-1	-1	-1	-1	-1	-1	-1	0	0	0	0	0	1	-1	-1	-2	-2	-2	-2	-1	-1
	0	0	0	0	0	1	0	0	-1	-1	-1	-1	-1	0	-1	-1	-2	0	-1	0	0	0	0	0	-1	0	-1	-1	-1	-1	-1	-1	-1	-1	-1
	0	0	0	0	0	0	0	0	-1	-1	-1	-1	0	0	-1	-1	-1	0	-1	-1	-1	0	0	-1	-1	0	0	0	-1	-1	-2	-1	-1	-1	-1
	-1	0	0	0	0	1	0	0	-1	-1	-1	-1	0	0	-1	-1	-2	-1	-1	-1	0	0	0	-1	-1	-1	-1	-1	-1	-1	-2	-2	-1	-1	-2
	-2	0	1	1	0	1	0	0	-1	-1	0	-1	0	0	-1	-1	-2	-1	-1	-1	-1	0	0	0	-1	0	0	-1	0	-1	-1	-2	-1	-1	-1
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	-2	0	0	1	0	1	0	0	-2	-1	-1	-1	-1	0	-1	-1	-1	-1	-1	-1	-1	0	0	-1	-1	-1	0	0	-1	0	-2	-2	-1	-1	-1
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	-2	0	0	0	0	0	-1	-1	-2	-1	-2	-1	-1	0	-1	-1	-1	-1	0	0	-1	0	0	-1	-1	0	1	0	0	0	-1	-1	-2	0	-1
	-2	0	1	0	0	0	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	0	0	0	0	-1	-1	0	-1	0	0	0	0	-1	-1	0	-1
	-3	0	1	0	0	1	-1	-1	-2	-1	-1	-1	-1	0	-1	-1	-1	0	0	-1	0	0	0	-2	0	0	-1	-1	0	0	-2	-2	-1	-1	-1
	-2	0	1	0	0	1	0	-1	-3	-1	-1	-1	-1	0	-2	-1	-1	0	0	0	0	0	-1	-1	0	0	-1	0	1	0	-1	-1	-1	-1	-2
	-1	0	0	0	0	0	-1	-1	-1	-1	-1	-1	0	0	-1	-1	-1	-1	0	0	-1	0	0	-2	-1	0	0	0	1	0	0	-1	-2	-1	-2
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0237 ←	-1	0	1	1	1	-1	-1	-1	-1	0	3	3	2	2	1	1	2	2	4	4	4	4	3	0	-1	0	0	0	1	1	1	0	0	0	0
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0248 ←	0	0	0	1	1	0	-1	0	0	-1	-1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	-1	0	1	0	1	0	0	0	0
	-2	-2	1	1	1	1	0	0	1	1	0	0	1	2	3	2	2	1	1	0	0	0	-1	-1	-1	-1	-1	0	0	1	-1	1	1	1	1

Figure 4. *A*, Matrix of echo amplitude data direct from processor for 35 depth levels and 35 minutes, including the example profiles from figure 3. Analysis matrix from which this was extracted was 60 depth levels by 240 minutes. Top row is depth in meters. Bottom three rows are number of data points in matrix at depth, mean value of points, and standard deviation of values. *B*, Normalized data from A. The mean for each depth level was subtracted from each point at that depth level, and the difference was divided by the standard deviation. Original values are integers and means; standard deviations and normalized values are decimal numbers that have been truncated for display.

10% below 220 m. The profile in figure 3B was taken 22 minutes after 3A and is an example of the display of targets in the AGC curve at approximately 50 m and 80 m. The profile in figure 3C was made 11 minutes after 3B, when the ship had passed over the target displayed in figure 3B.

The decline in "percent good" profiles in the ensemble decreases the precision proportional to the square of the number of good profiles. This means that at some depth below the ship, there will be essentially no information on the pattern of zooplankton distribution. The depth at which this happens has not been determined, and all nonrandom pattern has been analyzed no matter at which depth it was detected in the 12- to 250-m range.

The compact binary record also includes temperature of the water at the transducer, time of day, course and speed of the ship, geographic position of the ship, and the settings of the ADCP console at the time the ensemble average was taken.

The original binary record was converted to ASCII code for analysis. Two text files were constructed in the laboratory from each original file created at sea. One file contains 4 hours of AGC echo-amplitude data, 240 1-minute ensemble averages at each of 60 4-m depth intervals (figure 4A). The other file contains the date/time group, latitude, and longitude for the ensemble at half-hour intervals. The mean and standard deviation of the 240 values at each depth were calculated. Within each depth, the mean was subtracted from the value, and the difference was then divided by the standard deviation (figure 4B). Each data set was smoothed by the weighting matrix (figure 5), which was selected to speed the contouring process and limit the number of contour segments stored (Eber 1987). Contours were drawn at the unit-positive values of 1 or above. For the purposes of this study, small positive and all negative values were discarded as noise or assumed to represent the positions of continuous rather than aggregated sources of backscattering. Schott and Johns (1987) also contoured anomalies of echo amplitude in a moored ADCP.

Data collected over the continental shelf were not used for interpreting the mean and standard deviation for normalizing. In general, the volume reverberation was elevated in waters shallower than 240 m. Thus in the first and last panels of figure 8, the depth-specific means and standard deviations were assembled from data profiles in which the bottom echo was excluded.

We attempted to use the global mean and standard deviation for the entire data set rather than use 4-hour averages. The effect was to pool heterogeneous data, increase the standard deviation, and reduce the sensitivity of the normalized values to spatial structure. It is possible that electronics drift, long-term instrument instability, or environmentally induced changes in the signal amplitude make the derivation of a representative global mean and standard deviation uninterpretable with the present amount of data. To study these instrumental problems further, one must convert to calibrated sound sources and receiver sensitivities (Flagg and Smith 1989).

a. WEIGHTING FACTOR

1	8	1
8	64	8
1	8	1

b. CORNER WEIGHTING

64	8
8	1

Figure 5. Weighting matrices for the smoothing operator that were used to prepare the grid of values for contour tracking. *a*, The contoured value replaces the central value in the 9 contiguous bins and consists of a weight of 64 for the central value, 8 for each on-side contiguous value, and 1 for each diagonal contiguous value. *B*, At corners or edges the weighting matrix is adjusted to the location.

The ship's velocity was estimated from the file of dates, times, and geographic position. The sequential geographic positions nearest to each half hour were evaluated for distance traveled in the elapsed time. The difference in latitude in degrees was multiplied by 60 to obtain nautical miles, and by 1852 to obtain meters in that plane. The difference in longitude in degrees was multiplied by 60 and the cosine of the latitude (about 0.85 at the latitude of this study) to obtain nautical miles, and by 1852 to obtain meters. The distance in meters was calculated as the square root of the sum of squares of the latitudinal and longitudinal differences.

Aggregations were arbitrarily defined as those shapes within the 1 standard deviation-contour, which contained a contour of 2 or more standard deviations. Aggregations were assigned an aggregation serial number. We also determined the shallowest and deepest depths of each aggregation.

To estimate the horizontal extent, we measured the proportion of the aggregation's horizontal extent relative to the half-hour interval of distance traveled. The aggregation was then assigned a horizontal width in meters. For example, if the aggre-

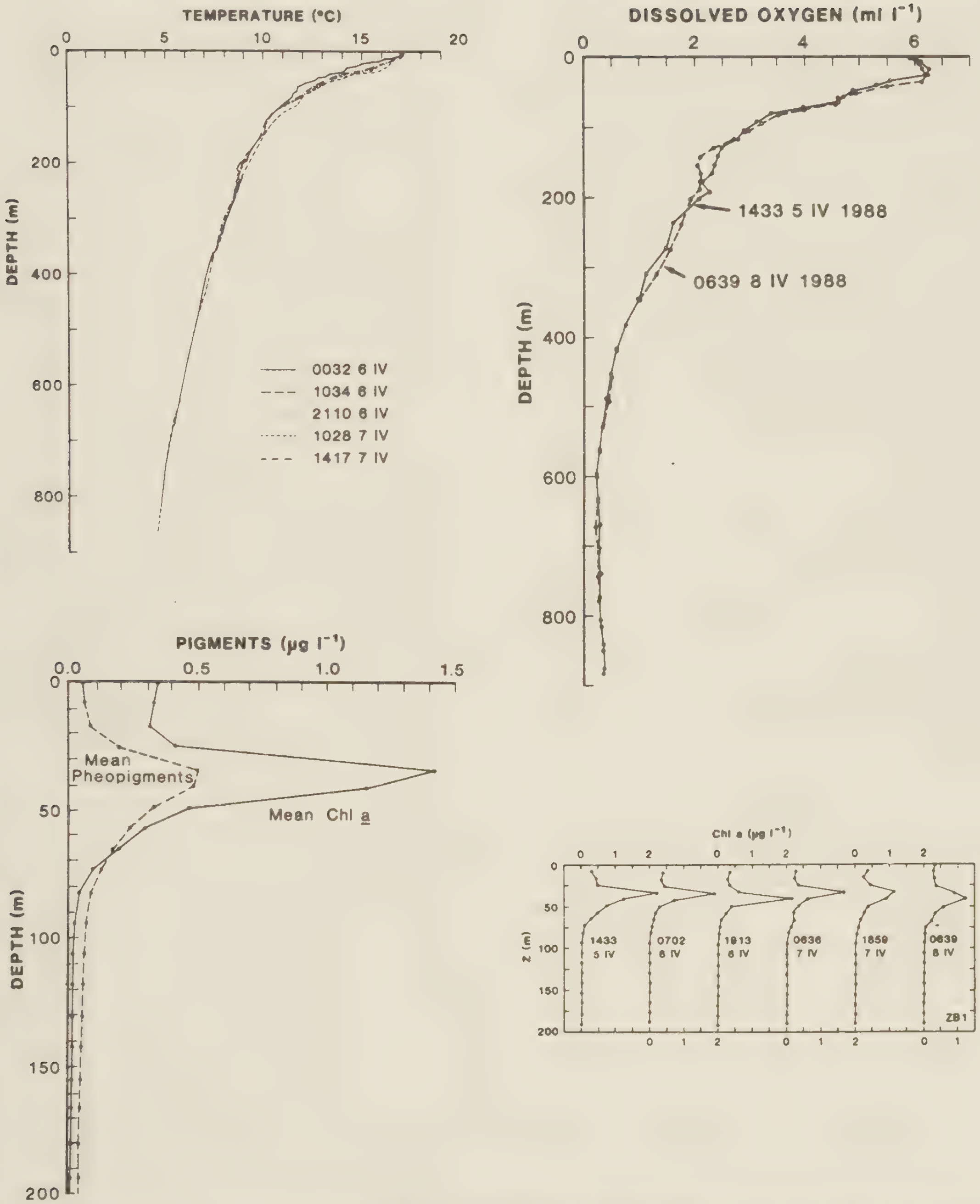


Figure 6. Vertical profiles. A, five temperature profiles; B, two dissolved oxygen profiles; C, means of six chlorophyll *a* and pheopigment profiles; D, six chlorophyll *a* profiles.

gation persisted for 10 minutes and the distance traveled in that half hour was 3200 m, the aggregation was said to extend 1070 m. The vertical plane area of each aggregation was estimated as the product of the vertical and horizontal dimensions. The sum of the vertical plane aggregation areas was estimated for each 4-hour period. The vertical plane area insonified was calculated by adding the ship's meters of progress in 8 half-hour intervals and multiplying by the depth of observation or 240 m. Comparison of the two values yielded an estimate of "coverage." Since there were no perfectly rectangular aggregations, the aggregation areas represent an overestimate varying from about 25% for inscribed circles to a factor of two or more for diagonally extended aggregations. Data exist for correcting this bias and for improving precision by more frequent evaluation of ship's speed.

RESULTS

Environmental Description

Vertical profiles of temperature, dissolved oxygen, and chlorophyll *a* can be characterized as exhibiting similarity in shapes and values among repetitions. Five temperature profiles taken between April 6 and 7 showed temperatures declining evenly, with some structure from 17°C at the surface to 5°C at 800 m (figure 6A). Deep oxygen profiles made near the beginning of the cruise (1433, April 5) and the end of the cruise (0639, April 8) showed similar gradients, with a subsurface shallow maximum and a deep minimum at about 600 m (figure 6B). Vertical profiles of pheopigments showed maxima of about 0.5 $\mu g\ l^{-1}$ at or near the depth of the chlorophyll maximum layer (figure 6C). Six chlorophyll casts had distinct subsurface maxima of 1–2 $\mu g\ l^{-1}$ between 35 and 45 m (figure 6D).

Vertical distributions of adult females of three species of calanoid copepods illustrate different types of behavior that influence acoustic sampling methods (figure 7). Because all three species were relatively abundant and are known to store lipids (Ohman 1988b), they should have affected backscattering at 307 kHz. *Calanus pacificus californicus* Brodskii was nonmigratory, remaining in the upper 50 m within acoustic range day and night (figure 7A). If the finer-scale vertical distribution of this species were constant over time and distance, a *C. pacificus californicus* layer would influence the mean but not the standard deviation of echo amplitude. *Eucalanus californicus* Johnson was also nonmigratory, but remained between 200 and 400 m day and night (figure 7B). Slight shifts in vertical distribution of *E. californicus* of a few tens of meters would bring it into and out of acoustic range, primarily affecting the standard deviation of echo amplitude. *Metridia pacifica* Brodskii underwent a distinct vertical migration (figure 7C). A daytime population mode at 200–150 entered the upper 50 m at night. Such a pronounced shift in vertical distribution would influence both the amplitude mean and stan-

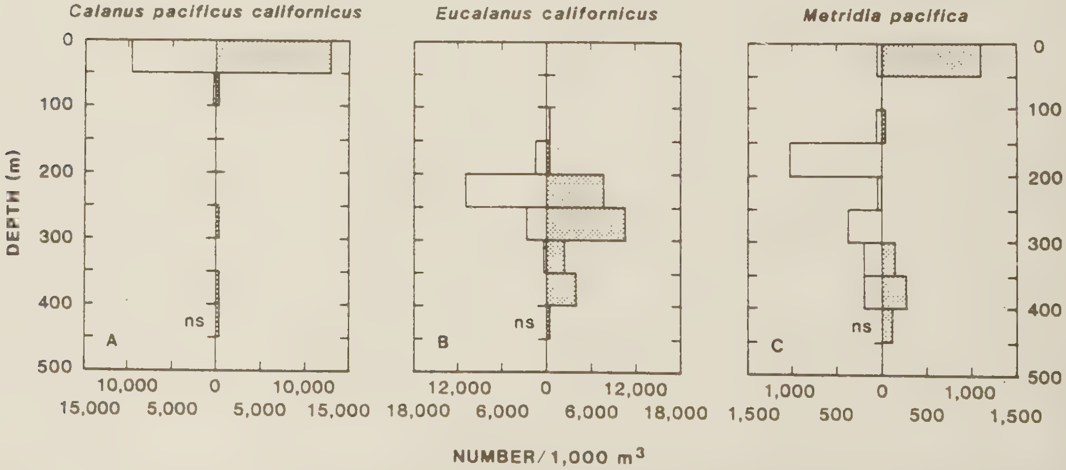


Figure 7. Day (open bars) and night (shaded bars) vertical distributions of adult females of the copepods *Calanus pacificus californicus* (A), *Eucalanus californicus* (B), and *Metridia pacifica* (C) on April 6, 1988. "ns" indicates that no sample was taken.

dard deviation. Note that a smaller segment of the *M. pacifica* population occurred at 400–300-m depth both day and night.

Euphasiid furciliae and adults, as well as other macrozooplankton taxa, also appeared in these samples.

General Appearance of Aggregations

There were no pronounced differences in the general appearance of aggregations between day and night. Both seem characterized by the appearance of shattered layers, shattered patches, and relatively smooth-edged patches. The physical size of the patches ranged from the threshold of detectability to relatively large at all depths at all times of day. The largest and most coherent aggregations were detected during the vertical migrations at dawn and dusk (figure 8C, F, I, L, O, R).

Migration and Migration Rates

Coherent aggregations during the entire period of migration were observed in one of three dusk records and two of three dawn records. On the dawn of April 7 the descending layer bifurcated into distinct layers (figure 8L). Estimates of maximum ascent rate ranged from 5 to 8 cm s^{-1}, and estimates of the maximum descent rate ranged from 3 to 4 cm s^{-1}. Aggregation densities exceeded three standard

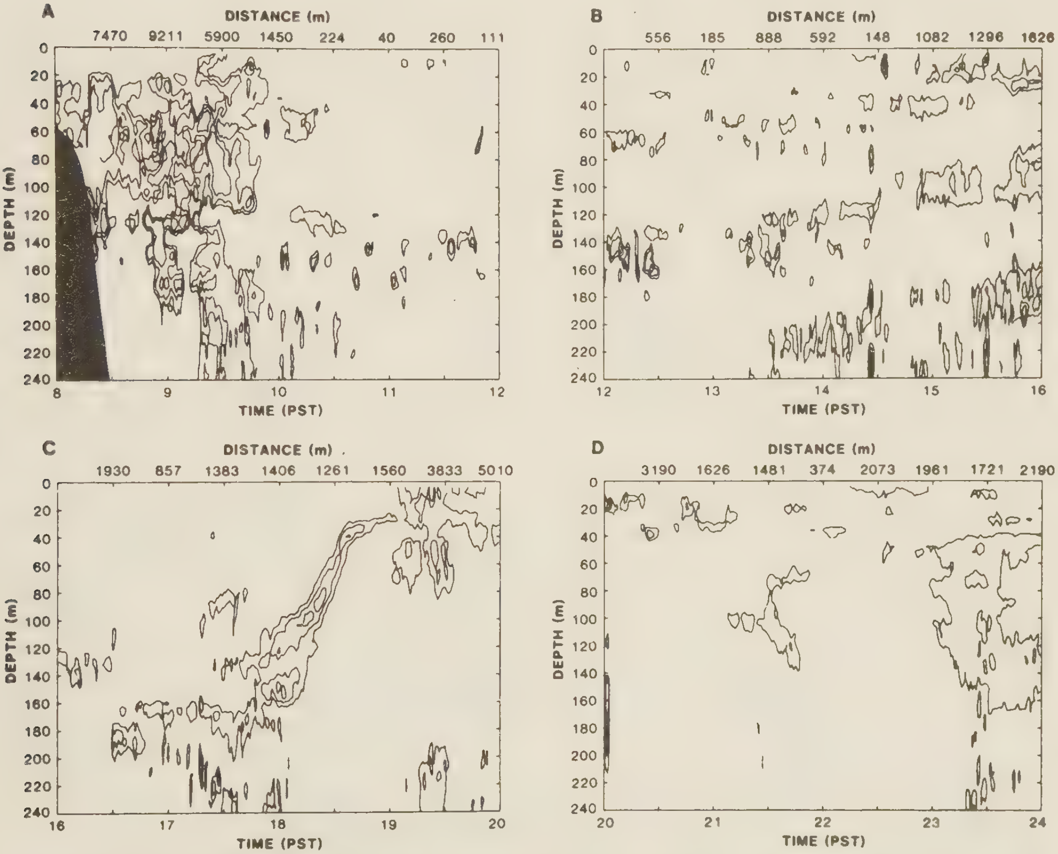


Figure 8 (continues on following three pages). *A–S* Each letter refers to a contoured data unit of 4 hours (less in 8S). The upper margin represents the straight-line distance between the ship's positions at the beginning and end of each half-hour interval. The figures are oriented on the page so that the day contours occupy the middle section, the dawn section for that calendar day is in the upper right, and the dusk section is in the lower left. The night contours are split between the upper left and the lower right. Contour interval is 1 standard deviation.

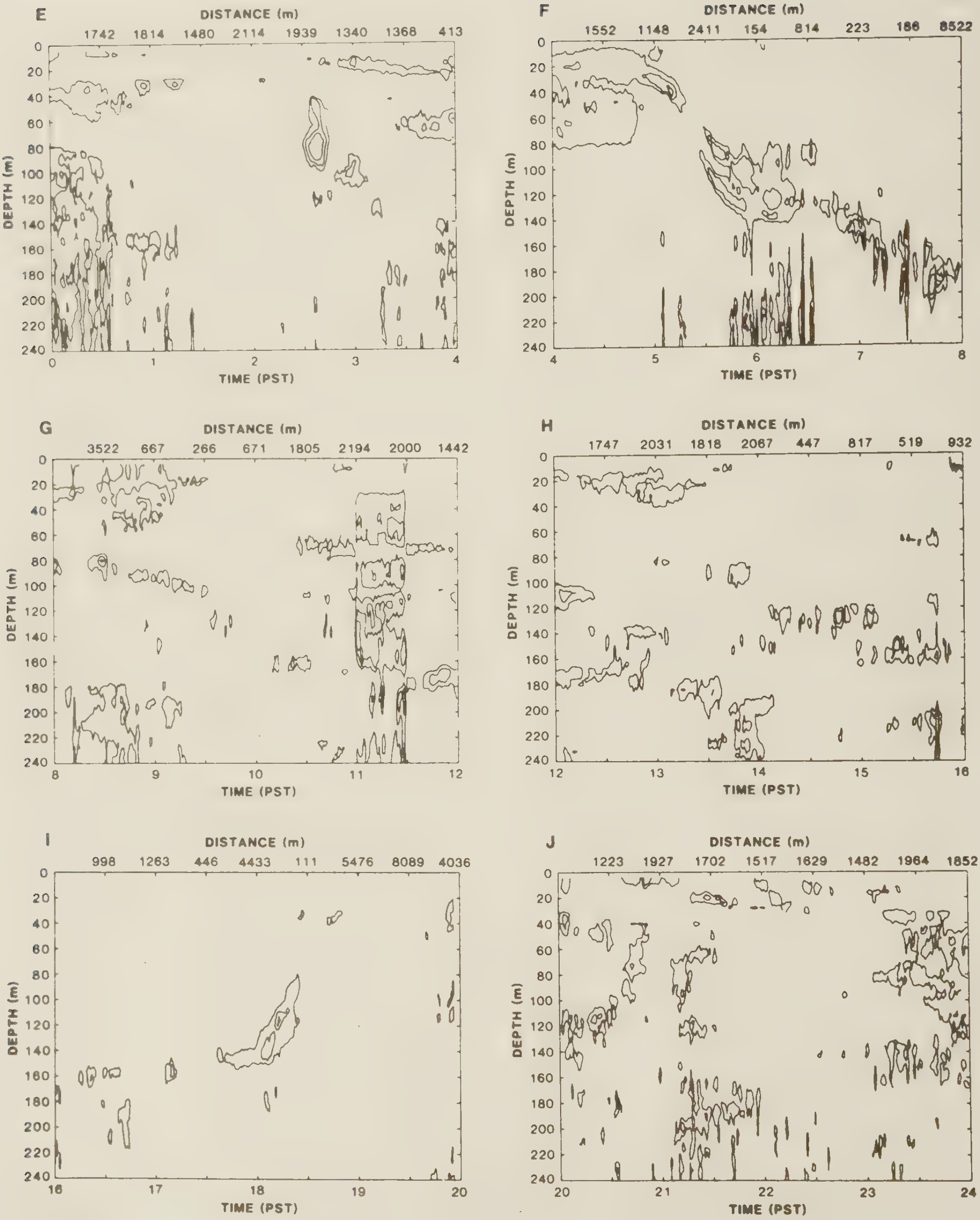


Figure 8 continued.

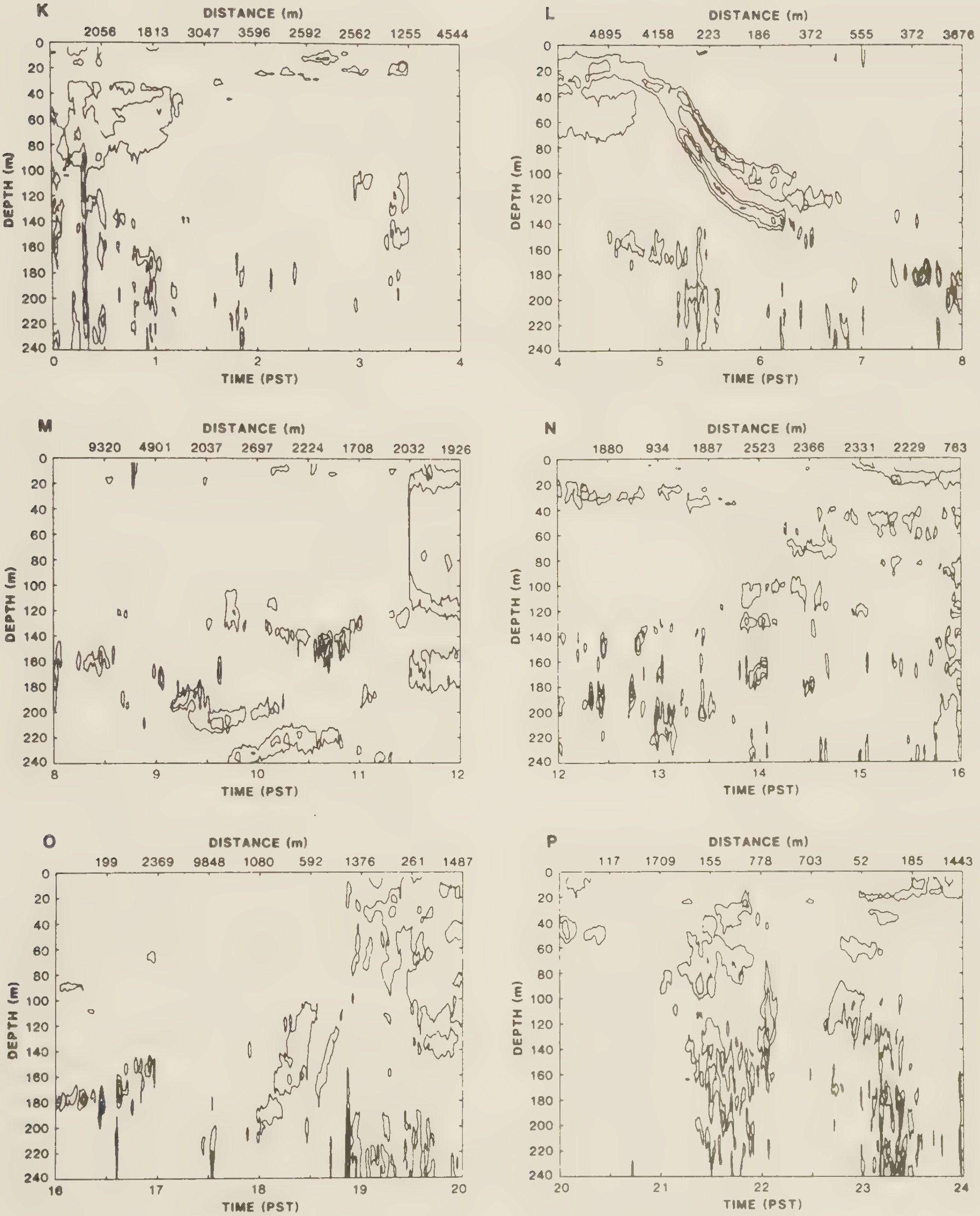
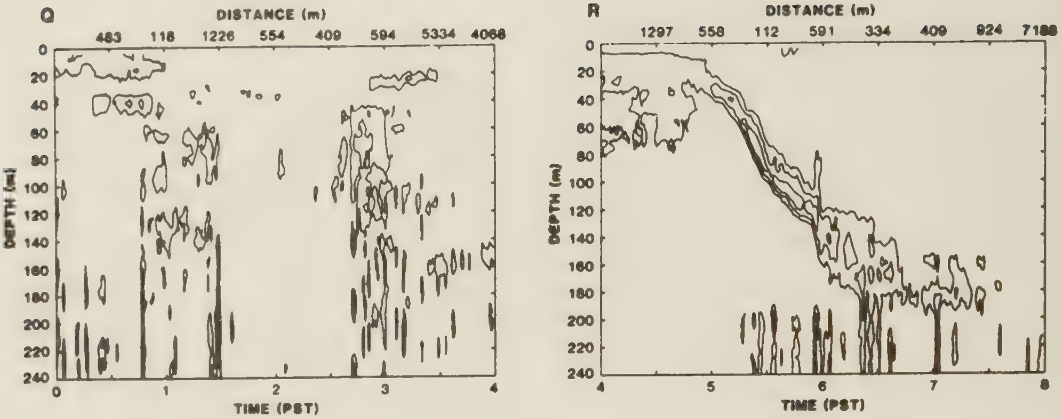


Figure 8 continued.



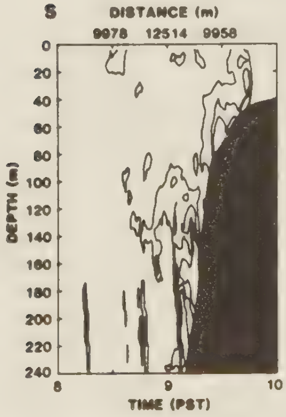


Figure 8 continued.

deviations above the mean in two of the three ascents and in all three descents.

Depth Distribution of Aggregations

Nearly twice as many of the 126 aggregations were detected at depth as near the surface (figure 9). The mean depth of aggregation is 134 m. At this stage of analysis it is not known if the cause of this distribution is simple or complex. The main cause of this imbalance is a surplus of aggregations at 180 m and 220 m and a deficiency of aggregations at 80 m and 100 m.

The simple explanation would be that this is the actual distribution of these aggregations. Complex explanations include (1) the width of the insonified volume increases at greater depths, increasing the chance of contact with patches; (2) some migrations from depth have destinations near the surface, where the ADCP process does not insonify; (3) the fore-and-aft dimension of the insonified volume at depth detects aggregations that have been insonified many times during each ensemble average in the lower level but that are missed by insonifying the gaps among patches during their residence in the upper level; (4) the general level of reverberation in the upper level is higher, and the use of normalized detection is less effective there than in the lower level, where the aggregations stand out against a lower reverberation background level; and (5) the aggregation behavior of the organisms leads to compact aggregations at depth but more diffuse and less-detectable aggregations at the surface. The small value at 240 m may reflect the approach of the absolute depth for detection of aggregations from the surface with 307-kHz sound. At depths over 150 m there may be undetected aggregations owing to decreased signal-to-noise ratios.

Vertical Dimensions of Aggregations

More than half of the aggregations are less than 50 m in vertical dimension (figure 10). The mean vertical dimension of the aggregations was 54 m.

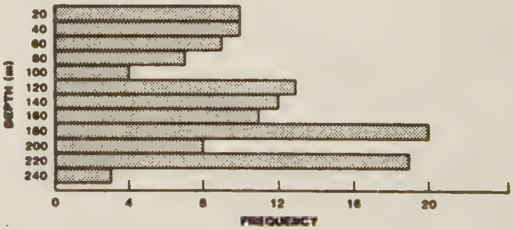


Figure 9. The depth distribution of aggregations.

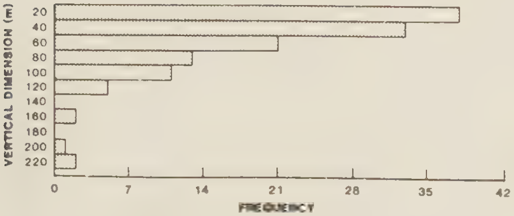


Figure 10. The vertical dimensions of aggregations.

Nearly 10% of the aggregations are more than 110 m in vertical extent. There has been no provision for excluding or estimating the incidence of aggregations that contact the upper or lower margin of the insonified volume; it appears unnecessary given the distribution of depths recorded here.

Horizontal Dimensions of Aggregations

The median horizontal dimension of aggregation is less than 750 m in the survey, and about 10% of the aggregations exceed 2250 m (figure 11). The arithmetic mean of the horizontal dimensions is 1268 m; the geometric mean is 519 m. This distribution is suitably approximated as a log normal distribution with parameters 6.251 and 1.440 (mean and standard deviation of ln values). The lower limit of detection of horizontal dimension is determined by ship's speed; at two knots (1 m s^{-1}) the lower limit would be 60 m; at 10 knots the lower limit would be 300 m. Much of this cruise involved the towing of plankton nets, and there was very little full-speed running between stations. Therefore the mode at horizontal dimensions less than 250 m may not be characteristic of cruise tracks at the higher speeds needed to cover wider geographic areas.

Horizontal Dimensions of Gaps between Aggregations

The median dimension of gaps between patches is less than 1500 m (figure 12). The arithmetic mean of gap is 2553 m; the geometric mean is 1120 m. The distribution is approximately log normal, with parameters 7.021 and 1.428. About 10% of the gaps are longer than 6500 m. Horizontal dimensions of gaps among patches appear to be about double the horizontal dimensions of the patches.

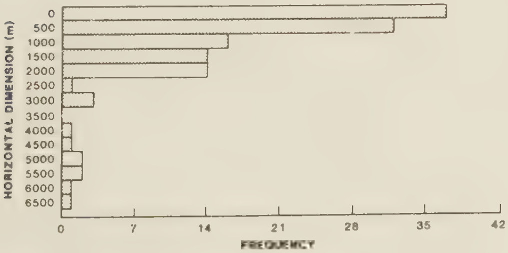


Figure 11. The horizontal dimensions of aggregations

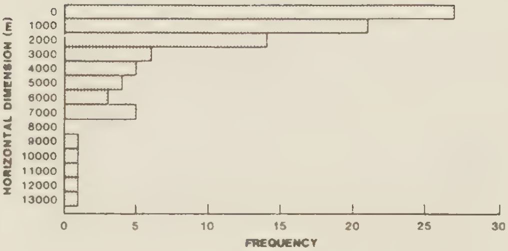


Figure 12 The horizontal dimensions of gaps between aggregations.

Coverage

There is a clear mode in the coverage statistic at 10% (figure 13). Two-thirds of the 19 observations occurred in this interval. Two of the 19 4-hour segments were more than 25% covered with aggregations as defined.

Continental Shelf and Slope

Plankton aggregations over the continental shelf, slope, and shelf-break area appeared in both crossings of that region. Since both passages occurred in daylight, this area may represent a special case for shallow daytime plankton aggregations. The points of contact of these aggregations and the bottom may be of considerable importance to the demersal organisms in those depth zones.

Summary

Some important features of aggregations have been described with a sample of 126 aggregations measured in 19 4-hour segments. Limited data indicate that there are important plankton aggregations at the break between the continental shelf and slope. The vertical section of the aggregations covers approximately 10% of the water column in the upper 240 m. The mean thickness of aggregation is

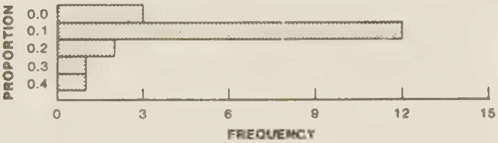


Figure 13. The distribution of proportion covered

54 m, and about half of the aggregations are less than 50 m in vertical dimension. The mean horizontal dimension is 1268 m, and about half are less than 750 m across. In the horizontal plane, the gaps between aggregations are about twice as large as the aggregations. Vertical migration of the aggregations can usually be detected at dawn and dusk, but it is possible to be between aggregations at the time of migration in this locality.

DISCUSSION

The primary results of this study are that a procedure for estimating the structure of plankton aggregations has been defined, and some preliminary data have been gathered in one habitat near the southern California coast over the San Diego Trough. Depth distributions, vertical and horizontal dimensions of the aggregations, and gaps between aggregations are relatively consistent. Although the number of sections is small, it is possible to estimate the coverage of the vertical section over this coastal area as about 10%. Some of the strongest and most clearly defined aggregations were detected at the time of vertical migration at dawn and dusk.

The 307-kHz sound used for this study is probably capable of detecting aggregations of larger copepods (Castile 1975), euphausiids, the gas bubble of physonect siphonophores, and mesopelagic fishes. The migration rates of the aggregations detected on this cruise are in the upper range for migrating copepods. Enright (1977) estimated migration rates of 1 to 5 cm s^{-1} for the calanoid copepod *Metridia pacifica* from sequential net tows taken near the present study site. In laboratory respirometer chambers the euphausiid *Euphausia pacifica* has been clocked at up to 9.7 cm s^{-1} (Torres and Childress 1983).

Several works have emphasized the interactions between the pelagic layers and the ocean bottom at the continental shelf, shelf-break, and slope (Isaacs and Schwartzlose 1965; Genin et al. 1988; Holliday 1987; and Pieper et al., in press). In the brief transects of the continental shelf and slope (figures 8A and 8S) in this paper, it would appear that this "enriched" region is worthy of more study. It is likely to be a region of high productivity of demersal fishes that depend on food advected in pelagic layers and the migrations of some of the biota.

Although the technique used for estimating the size of patches is fundamentally different from that used by Greenlaw and Pearcy (1985), the gross appearance and vertical and horizontal dimensions of the patches are similar. The Greenlaw and Pearcy study was conducted with a single transducer and a fully calibrated system in the amplitude domain. Therefore the patches could be defined in absolute acoustic units by measuring contours at 5-dB intervals. From formal spatial spectral analysis, Greenlaw and Pearcy concluded that the vertical dimensions were of the order of tens of meters, and horizontal dimensions were km-scale. Our conclusions were based on statistical manipulation of unquantified amplitude domain acoustic signals, which appeared to be stable for short periods (4 hours). Our spatial scales were determined by direct measurement of arbitrary contour drawings, with contours placed at 1-standard-deviation intervals. In most of the drawings for this paper, this would involve 2–3-dB spacing for contours.

The horizontal dimension of plankton aggregations and of gaps between aggregations may be compared to fish schools, primarily the omnivorous planktivore northern anchovy (*Engraulis mordax*). In figure 14 are plotted the cumulative distributions of patch and gap dimensions from this study, a distribution of fish school sizes (Smith 1981), and the distribution of fish school group sizes (Fiedler 1978). Also, Star and Mullin (1981) described critical length scales for distributions of copepod stages and species, and found kilometer-scale aggregations to be the rule at a depth of 35 m. The slopes of the cumulative curves are lower for the patches and gaps than for the schools and school groups: one may infer from this that nekton spatial structures are under more behavioral control than the plankton aggregations.

It is clear from the size and intensity of the planktonic structures that considerable invasive sampling, with precise vertical and horizontal control of nets or pumps, will be necessary for studying the dynamics and interactions of these populations. The tactical deployment of such samplers directed by integrative acoustic devices like the ADCP will materially aid in understanding the primary interactions among schools and school groups of planktivorous fishes. In particular, the joint use of ADCP and directed sampling devices will be needed to model the foraging strategy of schooling fishes, and their search for, and effect on, the plankton aggregations to explain the relationship among spatial scales of primary production, secondary production, and the production of fishes.

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We thank the participants on ZB1, including the captain and crew of the R/V *New Horizon*, for their assistance. E. L. Venrick coordinated the analysis of

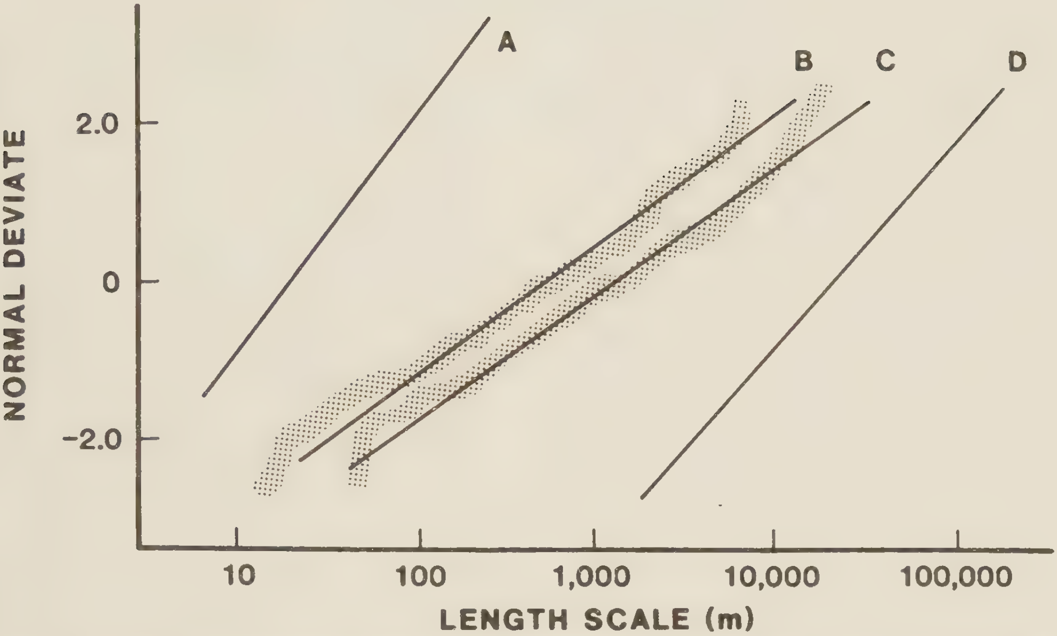

Figure 14. Comparison of the cumulative frequency distribution of horizontal dimensions of (*A*) fish schools (Smith 1981); (*B*) plankton aggregations, (*C*) gaps between plankton aggregations; and (*D*) fish shoal groups (Fiedler 1978). In curves B and C, a straight line has been fitted to the experimental data, which is represented with shading.

chlorophyll samples. Support came from the UC Ship Funds Committee and grant RM 252-S (to MDO) from the UCSD Academic Senate. We appreciate the assistance of Andrea Calabrese in data processing and data management. We also thank Ken Raymond and Roy Allen for drafting the figures and James Wilkinson for his help. Loren Haury and D. Van Holliday read the manuscript. Three reviewers also helped improve this manuscript.

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8970

Comparison of the Mortality Rates of Pacific Sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, Eggs off Peru[1]

Paul E. Smith, Haydee Santander, and Juergen Alheit

ABSTRACT: Egg production and mortality rates were estimated for populations of Pacific sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, off north and central Peru for August to September 1981. Peruvian anchovy spawned in the entire inshore region, principally within 56 km (30 nmi) of the coast. The Pacific sardine spawned extensively in the northern and southern inshore regions but not in the central region. While spawning of the two species coincided at the regional scale, at the sample scale, the occurrence of eggs of the two species was statistically independent. The egg production rate of Peruvian anchovy was about double that of sardine. The mortality rate of Pacific sardine eggs was much higher than that of Peruvian anchovy. The egg mortality rates of Peruvian anchovy and Pacific sardine were unchanged at stations where Pacific sardine and Peruvian anchovy eggs occurred together, relative to where the two species' eggs occurred separately. Results of this study are used to evaluate cannibalism as a population limiting mechanism. Cannibalism accounts for about 30% of egg mortality in anchovy. Because of the schooling habit of sardines and anchovies, cannibalism, though large-scale, may not vary enough with population size to explain variations in recruitment.

In their review of clupeoid biology, Blaxter and Hunter (1982) emphasized the need to estimate instantaneous rates as the "only way to establish a satisfactory linkage between the fish and their environment." These instantaneous rates include production of spawn (Lasker 1985) and mortality rate of the eggs and larvae. Predation is thought to be an important cause of mortality, and one form of predation, cannibalism, has been proposed as a mechanism for establishing an upper limit to population density (Ricker 1954; Hunter and Kimbrell 1980; MacCall 1980; Alheit 1987; Pauly and Soriano 1987) of filter-feeding, pelagic spawning, schooling coastal pelagic fishes.

MacCall (1983) has described abundance as a composite of population density and geographic extent: northern anchovy, *Engraulis mordax*, appears to have a central area where density-dependent processes have their greatest effect on local density and a peripheral area where density-dependent processes are less important. Reductions of density in the central area result in contractions of the population to the central area for Pacific sardines, *Sardinops sagax*, (Murphy 1966) and northern anchovy (MacCall 1980). Off California both sardines and anchovy contract to the same area (Ahlstrom 1967).

Microstructure in the sea plays an important role in interaction of predator and prey (Lasker and Smith 1977) at the embryonic and larval stages (Smith 1973; Vlymen 1977; Theilacker 1987). There may also be rapid changes in the microstructure due to dispersal (Smith 1973; Smith and Hewitt 1985b). McGurk (1987) has proposed that small-scale pattern may make mortality rates proportional to patchiness rather than inversely proportional as originally suggested by Brock and Riffenburgh (1960).

Subsequent variations in recruitment may be caused by environmental influences on first-feeding larvae (Hjort 1926; Lasker 1975, 1978, 1981; Peterman and Bradford 1987), and recruitment is regulated by the interaction of growth and mortality rates of juveniles (Shepherd and Cushing 1979; Smith 1985; Butler 1987). Peterman et al. (1988) demonstrated that in a selected subset of years there was no relationship be-

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Contribution No. 171 of the Alfred-Wegener-Institute for Polar and Marine Research.

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tween the abundance of northern anchovy larvae off California at 20 days of age and the recruitment at age 1. It had previously been shown that, for a shorter time series in the same habitat, Pacific sardine recruitment at two years old varied 15-fold, while the egg abundance in the year of origin for the same years varied only 3-fold (Smith 1978).

A major barrier to estimating egg mortality in pelagic schooling fish is the tendency of these fish to aggregate closely for external fertilization of spawn (Leong in press), presumably to conserve sperm and ensure high fertilization rates. The eggs are subsequently dispersed by turbulent diffusion (Smith 1973; Smith and Hewitt 1985a). Schooled spawning, with its spatially intense pattern, imposes a high sample variance on the younger eggs, and dispersal reduces the sample variance with time (Smith and Hewitt 1985a).

Precise estimation of survival and egg production rates requires large numbers of samples. The intensity of patchiness is indicated by the maximum values for egg counts. Smith (1973) observed that the concentration of Pacific sardine eggs off California was a maximum of 3,100 eggs/m^2, and Hunter (1980) observed that a concentration of 1 d old northern anchovy eggs was 4,600 per m^2. Walsh et al. (1980) reported the results of sample analyses of Peruvian anchovy eggs along the Peruvian coast. From five samples at lat. 10°S and seven samples at 15°S, they found a maximum value of 11,500 Peruvian anchovy eggs/m^2, and they also found Peruvian anchovy larvae at 100 and 200 per m^2. Santander et al. (1982) reported on Peruvian anchovy and Pacific sardine off Peru. For Peruvian anchovy, they found a maximum egg concentration of 107,376 eggs/m^2 (all ages). This count was from the largest of 911 ichthyoplankton tows with Peruvian anchovy eggs out of 4,028 Hensen net samples between 1966 and 1979. For Pacific sardine off Peru, the maximum egg concentration was 58,500 eggs/m^2 (H. Santander[2]). This count was from the same set of 4,028 tows.

Pacific sardine spawning off Peru has been essentially stable between 1978 and 1981 (Santander 1981). What are the implications for selection of spawning sites for the two pelagic spawners? Do the two species partition the environment into separate spawning areas or do they concentrate on oceanic sites favorable to both? What are the relative rates of egg production and mortality where they co-occur?

In this paper we describe regional and interspecific differences in egg production and mortality off Peru. The Peruvian anchovy data used for this paper have already been used for estimating egg production of the Peruvian anchovy population off north and central Peru (Santander et al. 1984). The Pacific sardine egg data off Peru are adequate for determining egg production per unit area, but contemporaneous adult reproduction rates are lacking; thus, sardine adult biomass has not been estimated.

METHODS

Cruise plan, sampling methods, laboratory methods, and data analysis have been described fully by Santander et al. (1984; an English version can be obtained from the author J. Alheit). Only a brief account of these methods is presented here.

The objective of the investigation was to encompass the Peruvian anchovy and Pacific sardine spawning grounds off northern and central Peru with an intensive grid of ichthyoplankton stations. The survey extended from Pisco (lat. 14°S) in the south to Punta Falsa (6°S) in the north. The background, a computer program for distributing the stations, and other technical details of the cruise plan are described in Smith et al. (1983). The sampling stations were distributed on transects perpendicular to the coastline. The inshore spacing of transects was 10 nmi. Thirty-five transects extended 30 miles offshore and 18 transects extended 90 miles offshore. On all transects the sampling stations were three miles apart. The total number of stations was 925. The area under investigation was subsequently divided into nine regions for some aspects of the analysis (Fig. 1).

Eggs were sampled with the CalVET net (CalCOFI vertical egg tow; Smith et al. 1985). Its mesh size was 333 μm, and its mouth area was 0.05 m^2. The net was towed vertically from a 70 m depth to the surface within 1 minute. The net filtered 3.5 m^3 of water.

Following sorting, the eggs were aged according to their developmental stage, the surface water temperature, and the time of day when the sample was collected. The following is a brief summary of the method for determining Peruvian anchovy egg production; a complete description of these techniques for northern anchovy is found in Picquelle and Stauffer (1985).

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[2] H. Santander, Instituto del Mar del Peru, Apartado 22, Callao, Peru, unpubl. data.

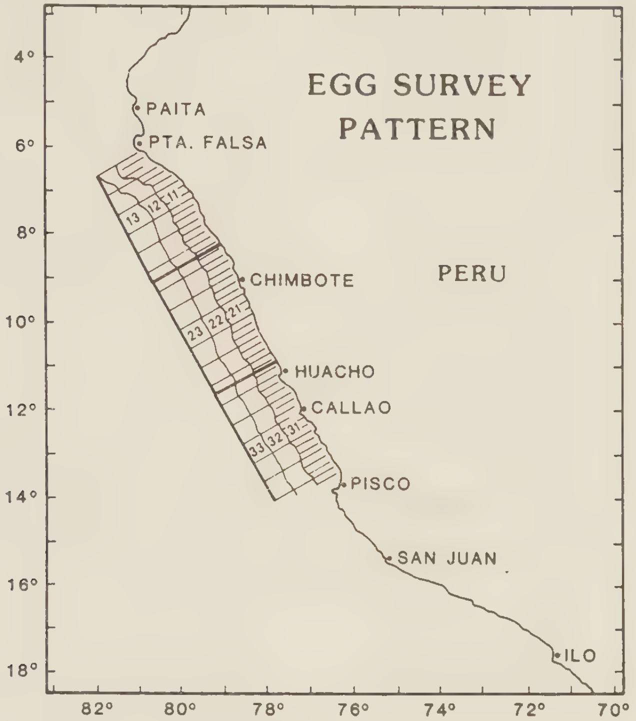

FIGURE 1.—Coastline of Peru and egg survey stations and statistical regions. Egg sampling stations are 3 miles apart in the cross-shelf plane. Regions for statistical summaries are coded. The first digit of each number refers to the north "1", central "2", or south "3" sectors of the coast. The second number refers to the inshore "1", offshore "2", or seaward "3" regions of each sector. In text, codes referred to as IMAR11, IMAR12, etc. to distinguish the codes from numbers. Original station positions and equations for plotting are in Smith et. al. (1983).

Anchovy and sardine eggs were grouped in 12 h intervals. Newly spawned eggs collected during the spawning interval and older eggs collected during hatching were eliminated from the calculations. The remaining egg counts were regressed on age to fit a mortality function of the egg data. The daily egg production was then estimated by zero intercept of the exponential mortality function. The following exponential model can be fit to the egg data by the nonlinear, least squares regression (Stauffer and Picquelle 1980[3]):

$$P_0 = P_i e^{-zt}$$

where P_0 = daily egg production;
P_i = number of eggs of age t_i sampled during the time interval t_i, t_{i+1};
t = time elapsed between spawning and the ith time interval; and,
Z = instantaneous daily rate of egg mortality.

The P_0 is the intercept of the exponential curve. The model assumes that all eggs are spawned and fertilized at an instant, that the eggs have a constant rate of mortality, and that the sampling was representative and includes all areas where eggs may be found.

RESULTS

Peruvian anchovy and Pacific sardine co-occur along the north and central coast of Peru

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[3] Stauffer, G. D., and S. J. Picquelle. 1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. U.S. Dep. Commer., NOAA, NMFS SWFC Adm. Rep. LJ-80-09, 41 p.

(Santander 1981). In 1981, the Peruvian anchovy egg distribution was essentially continuous near the coast, with some extension offshore to 30 miles offshore of Chimbote (Fig. 2). In contrast, the Pacific sardine eggs occurred in two groups separated by about 120 nmi between Huacho and Chimbote. The Pacific sardine eggs extended farther offshore than Peruvian anchovy eggs and were not as abundant in the nearshore stations.

Of the 925 samples that were taken (Santander et al. 1984), 575 came from the inshore regions IMAR11, IMAR21, and IMAR31 (Fig. 1). Twenty-one percent of the samples in the inshore regions had both Peruvian anchovy and Pacific sardine eggs, 32% had only Peruvian anchovy eggs, 18% only Pacific sardine eggs, and 28% had neither Peruvian anchovy nor Pacific sardine eggs (Table 1).

TABLE 1.—Number (% in parentheses) of plankton hauls in which Peruvian anchovy, *Engraulis ringens*, and/or Peruvian sardine, *Sardinops sagax*, eggs occurred in the three inshore regions.

Region	Both anchovy and sardine	Anchovy only	Sardine only	Neither anchovy nor sardine	Total
IMAR11	51 (27)	26 (14)	65 (35)	45 (24)	187
IMAR21	34 (17)	91 (46)	18 (9)	54 (27)	197
IMAR31	36 (19)	69 (36)	22 (12)	64 (34)	191
Total	121 (21)	186 (32)	105 (18)	163 (28)	575

There were fourfold fewer ½ d old Pacific sardine eggs per station in the samples with Pacific sardine eggs in the absence of Peruvian anchovy eggs as compared with Pacific sardine eggs per station when Peruvian anchovy eggs were also present (Table 2). By way of contrast, the Peruvian anchovy eggs appeared to be equally abundant, with or without Pacific sardine eggs in the sample. There appeared to be a trend of Pacific sardine egg abundance in absence of Peruvian anchovy eggs becoming proportionally less abundant with age, but the trend was mostly concealed by the high standard errors of the two categories. Of course these rates cannot be known precisely from exploratory data analysis; the absolute rates would have to result from specifically designed studies with higher precision.

On a regional basis, sardine egg production was highest in the northern region (IMAR11), negligible in the central region (IMAR21), and higher in the southern region (IMAR31, Table

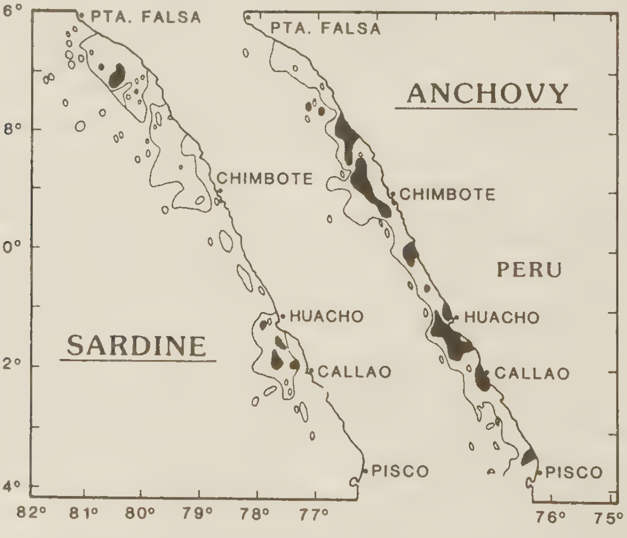

FIGURE 2.—Pacific sardine (left) and Peruvian anchovy (right) egg abundance in August to September 1981. For each species, shaded areas indicate where their eggs were taken at densities of 1–100 eggs/0.05 m^2, and black areas indicated 101 or more eggs/0.05 m^2. Peruvian anchovy data has also been mapped in units of eggs per square meter in Santander (1987, Map No. 78, p. 204).

TABLE 2.—Mean number of Peruvian anchovy, *Engraulis ringens*, and Pacific sardine, *Sardinops sagax*, eggs per station by age group. The age group code A1 refers to eggs aged in the first half of the first day after spawning; A2 refers to eggs aged in the second half of the first day; B1 refers to eggs aged in the first half of the second day; and B2 refers toe ggs aged in the second half of the second day. "All" refers to all stations where that species' eggs were present. Only the inshore regions (IMAR11, IMAR 21, IMAR31) combined were considered for estimation of these parameters. "Both" refers to those stations where eggs of both species were present. "Only" refers to stations where that species' eggs were present.

Age group	Variable	Anchovy All	Anchovy Both	Anchovy Only	Sardine All	Sardine Both	Sardine Only
A1	Mean	62.92	67.49	59.11	19.53	26.58	6.66
	SE	8.70	12.70	11.99	7.01	10.70	2.33
A2	Mean	22.90	36.07	16.32	6.73	12.35	2.16
	SE	3.73	9.34	2.93	1.84	3.91	0.66
B1	Mean	31.05	37.59	26.60	2.14	2.88	0.77
	SE	5.35	7.92	7.25	0.48	0.71	0.33
B2	Mean	9.36	11.15	8.46	1.32	2.62	0.23
	SE	1.31	2.37	1.58	0.57	1.24	0.12

3). Peruvian anchovy egg production was relatively even in all sectors of the inshore region. The mortality rates of both Pacific sardine and Peruvian anchovy were highest in the northern region. Pacific sardine mortality rates were higher than Peruvian anchovy mortality rates in each region.

Mortality rates of Peruvian anchovy and Pacific sardine eggs were not higher where the eggs occurred in the same samples (Table 4). Pacific sardine egg production, in areas where Pacific sardine eggs were not accompanied by Peruvian anchovy eggs in a sample, was only a third of that where the two species' eggs were found together. As in the case of abundance, Peruvian anchovy egg production and mortality rates do not appear to be related to the presence of Pacific sardine eggs in the sample.

The spatial overlap of the Pacific sardine spawning areas and Peruvian anchovy spawning areas cannot be distinguished from randomness. The probability that a 0.05 m^2 sampler will miss a Peruvian anchovy egg patch was 0.47 and for a Pacific sardine egg was 0.61 in August–September of 1981 off northern and central Peru. The joint probability of a sampler of this size missing both species' eggs as estimated from the product of the individual species' probabilities was 0.29. The measured probability of missing both species was 0.28 (Table 1). Therefore based on occurrence in a 0.05 m^2 mouth area sampler, the small-scale spatial distribution of Pacific sardine and Peruvian anchovy eggs was indistinguishable from total independence of each other.

In summary, the results of this study show that Pacific sardines and Peruvian anchovies spawned along the coast over the latitudinal extent of northern and central Peru with the preponderance of spawning within 30 nmi of the coast. The production rate of Peruvian anchovy eggs per unit area (104 eggs/0.05 m^2 d^{-1} was about double that for Pacific sardine (56 eggs/0.05 m^2 d^{-1}) and the mortality rate of Peruvian anchovy eggs ($z = -1.12$ or 67% d^{-1}) was substantially lower than that of Pacific sardine ($z = -2.12$ or 88% d^{-1}). The highest mortality rate for both species occurred in the northern region (IMAR11). For the Pacific sardine in the northern region, the instantaneous rate was −3.88 (98% d^{-1}). For the Peruvian anchovy in the north, the instantaneous rate was −2.14 or 88% d^{-1}. Mortality rates of Peru-

TABLE 3.—Regional egg production (P_0) and mortality rates (Z) of Pacific sardine and Peruvian anchovy as estimated by a nonlinear least squares procedure assuming an exponential model.

Species	Category	Production (SE) eggs/0.05 m^2/d	Mortality (SE) daily instantaneous
Sardine	IMAR11	16.6 (2.6)	3.88 (0.39)
	IMAR21	0.4 (0.1)	1.28 (0.35)
	IMAR31	8.7 (1.5)	1.47 (0.28)
Anchovy	IMAR11	22.0 (9.2)	2.14 (0.83)
	IMAR21	23.7 (6.7)	0.93 (0.36)
	IMAR31	17.0 (4.9)	0.90 (0.35)

TABLE 4.—Egg production (P_0) and mortality rates (Z) of Pacific sardine and Peruvian anchovy for all inshore regions where samples are positive for either species. "All" refers to all stations where eggs of that species were present. "Only" refers to stations which were positive for one species but the eggs of the other species were absent. "Both" refers to stations where eggs of both species were present.

Species	Category	Production (SE) eggs/0.05 m^2/d	Mortality (SE) daily instantaneous
Sardine	All	56.3 (3.2)	2.12 (0.10)
	Only	20.2 (0.4)	2.22 (0.03)
	Both	64.1 (9.2)	1.75 (0.22)
Anchovy	All	104.7 (37.2)	1.12 (0.44)
	Only	109.9 (47.0)	1.35 (0.58)
	Both	104.0 (25.5)	0.90 (0.28)

vian anchovy and Pacific sardine eggs were not higher where the eggs occurred in the same sample.

DISCUSSION

In this section we will discuss Pacific sardine and Peruvian anchovy egg production and mortality off Peru, fundamental statistical problems to be overcome in future studies, some other mechanisms of population control, and egg cannibalism and population control in pelagic spawning, schooling coastal pelagic fishes.

Pacific Sardine and Peruvian Anchovy Egg Production and Mortality

It appears that Pacific sardines and Peruvian anchovies off Peru select the same large-scale sites for egg deposition but select independently of each other at the small scale. While the eggs of both species were concentrated in the inner 30 miles of the survey pattern (Fig. 2), the probability of occurrence on a sample-by-sample basis was not demonstrably different from independent distributions for the two species (Table 1).

Where Pacific sardine and Peruvian anchovy eggs occurred together, Peruvian anchovy egg production rates were equal to those sites where Peruvian anchovy eggs occurred alone, but Pacific sardine egg production rates were higher at co-occurring sites than those sites where only Pacific sardine eggs were taken. Mortality rates where both occurred were marginally lower than where each occurred separately: this implies that the proximity of the adults of the other species does not affect the egg mortality rates. The northern region had the maximum rate of mortality for both Peruvian anchovy and Pacific sardine. The northern region had also the maximum regional rate of production for Pacific sardine, virtually equal to the Peruvian anchovy egg production rates of the other two regions (Table 3).

In all regions, the Pacific sardine mortality rate was higher than the anchovy mortality rate. Of an estimated 2,094 eggs produced/m^2 d^{-1} by Peruvian anchovy, 1,410 (67%) died on the first day. Of an estimated 1,126 eggs produced/m^2 d^{-1} by Pacific sardine, 990 (88%) died on the first day. We suggest two explanations for the cause of higher mortality rate of Pacific sardine eggs relative to Peruvian anchovy eggs in the same region: Moser[4] pointed out that the ovoid shape of the anchovy egg (0.7 × 1.4 mm) as compared with the spherical sardine egg (1.4 mm) may reduce the chance of being eaten by filter-feeders. Author H. Santander has observed that sardine eggs are more delicate to handle in the laboratory. This may mean that the integument of the sardine egg is more susceptible than the anchovy egg to physical damage by predators in the sea. Their susceptibility to damage might also explain their apparent low incidence in juvenile and adult sardine and anchovy stomachs, because broken eggs might not be detected (Santander et al. 1983).

Fundamental Statistical Problems

Errors in the estimation of the slope parameter induce errors of the same sign in the intercept parameter: for this reason there are major problems in comparing adult spawning biomass concentration derived from the intercept parameter and egg mortality rate derived from the slope parameter. Thus, for the purpose of this paper, the comparison of spawning biomass concentration and egg mortality is not reported as a result of this research. Instead, Figure 3 and Table 6 are points of discussion. The data come from a plan for stock assessment and as such are not definitive on the question of biomass concentration and egg mortality rate. The relationship is suggestive, however, and may be used to design a study of cannibalism that is not statistically confounded.

The statistical problem of patchiness (Taft 1960), encountered when estimating the abundance of fish eggs, becomes more severe when estimating production and mortality of eggs because the intensity of patchiness changes with age (Smith 1973, 1981; Smith and Hewitt 1985a, 1985b; McGurk 1987). Since the mortality estimate requires the arithmetic means (Southwood 1978), log transformation to stabilize variance is not used.

Egg production (P_0) and mortality rate (Z) are determined using the exponential mortality model (Picquelle and Stauffer 1985). It has been determined that the midpoint of spawning is at 2200 hours but samples from the spawning interval are biased (Smith and Hewitt 1985a). The intercept and mortality rate could be systematically underestimated if the actual mortality rate in the initial period was higher owing to an interaction between local density and mortality rate on eggs at the highest distributional densities (McGurk 1987).

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[4] H. G. Moser, Southwest Fisheries Center La Jolla Laboratory, Natl. Mar. Fish. Serv., La Jolla, CA 92038, pers. commun. May 1983.

The Central Limit Theorem requires independence among sample values. With the spawning of Pacific sardine and Peruvian anchovy off Peru compressed against the coast in a 30 mile band in 1981, abundance estimates from stations separated in the cross-shelf dimension at 3 mile intervals are not likely to be independent. The effect will be an underestimate of sample standard error of the mean (Table 2). The degree of the same type of error in the along-shelf plane was probably smaller because the transects are 10 nmi apart. Also the collection of sites used for the estimates of abundance of 1 and 2 d old eggs in the first half of each day (A1 and B1 in Table 2) are from different stations from those used for estimates of abundance of 1 and 2 d old eggs in the second half of each day (A2 and B2 in Table 2).

Other Mechanisms

Egg cannibalism is probably only one of several possible population controlling mechanisms in anchovies. For example, cannibalism could occur at life stages other than the egg stage. There have been recent observations, in the laboratory, of older anchovy larvae consuming younger larvae (Brownell 1985). In these observations, the larvae became more vulnerable as pigmentation formed in their eyes and integument.

Energy demands for egg production and spawning could lead to aggregations of adults where food production and, coincidentally, egg mortality are both high. That, in both Pacific sardine and Peruvian anchovy, higher rates of egg mortality and egg production occurred in the same region (IMAR11) seems to support this view. Lastly, from laboratory observations, northern anchovy larvae, only a day old, may seek and maintain position in patches of *Gymnodinium*, making these larvae vulnerable to enhanced feeding activity by many other organisms in the same patch or layer (Hunter and Thomas 1974).

Egg Cannibalism and Population Control

For the northern anchovy, *Engraulis mordax*, Peterman et al. (1988) concluded that the size of the recruited stock is not determined in the first 20 days following spawning. On the other hand, Pauly[5] concluded that egg mortality due to cannibalism by the adult stock is a primary density dependent control on recruitment in the Peruvian anchovy, *Engraulis ringens*. Smith (1985) lists three situations in which cannibalism by schooling pelagic spawners would be an effective population controlling activity: 1) directed filtering behavior on dense aggregations of eggs; 2) encounter with other schools' patches of eggs; and, 3) anchovy population switching from biting to filtering behavior.

Directed Filtering

In the first few hours after spawning, before much dispersal has taken place, directed filtering could be an important source of mortality (Smith and Hewitt 1985b; McGurk 1987). Hunter and Dorr (1982) found that adult northern anchovy filtering was induced by 5 northern anchovy eggs/L and sustained by 1 or 2 eggs/L in laboratory tanks. Given that the level of artificial feeding is higher for laboratory animals and that probably the quality of water for sensing prey is lower, these thresholds may be higher in the laboratory than in the sea. One disadvantage of this mechanism for population size control is that, because of proximity, the most likely school to encounter the newly spawned patch is the school from which the spawn was produced. Santander et al. (1983) found that Peruvian anchovy eggs < 2 hours old were overrepresented by a factor of three in the stomachs of Peruvian anchovy relative to their incidence in the sea. In a typical spawning school (Santander et al. 1984; Alheit 1985), there would be 10 times as many Peruvian anchovies feeding on eggs than females spawning eggs. While the mortality rate might be sufficient, it is difficult to seen how a change, in population size or in density over thousands of square kilometers, could materially affect a species grazing for a few hours on its own eggs over a range of a few hundred meters. This source of mortality, although large, may not be sufficiently variable with population density to control recruitment.

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[5] The estimate of instananeous mortality "z" derived by Pauly (1987) is strongly biased downward at low mortality rates but should still be valid at high levels of parent stock. Daniel Pauly, International Center for Living Aquatic Resources Management, Manila, Philippines, pers. commun. March 1989.

Encounter

Incidental filtering of eggs by encounter of other schools' patches of eggs would appear to be a direct mechanism for parental control of recruitment rate and population density. If one combines the information on egg cannibalism rate by Alheit (1987) and the demographic influence on population annual fecundity reported by Pauly and Soriano (1987) (Table 5), one can see that the effective fecundity (eggs hatched after cannibalism) would be low when the stock was composed primarily of juveniles and first-year spawners.

TABLE 5.—Age-specific rates of cannibalism and egg production for anchovy.

Age (yr)	Anchovy egg production[1] (eggs/g/d)	Anchovy egg consumption[2] (eggs/g/d)	Effective fecundity (eggs/g/d)
Juveniles[3]	0.	9.3	−9.3
1	3.9	9.3	−5.4
2	9.0	9.3	−0.3
3	15.7	9.3	6.4
4	18.4	9.3	9.0

[1] Pauly and Soriano 1987
[2] Alheit 1987
[3] Ciechomski 1967

Switching

It is also possible for cannibalism to interact indirectly with population density. An indirect method for population control is evident if one considers a system where the anchovy prefer to feed by biting relatively large zooplankton and where filtering occurs only when large zooplankton are low in abundance (O'Connell 1972). Under these circumstances predation by anchovy on the major herbivores could result in a larger standing crop of phytoplankton and in increased rates of anchovy filtering (MacCall 1980). In the course of switching to a preponderance of feeding by filtering, the anchovy would inadvertently filter anchovy eggs at a higher rate.

Egg production rate was sixfold higher in Peruvian anchovy compared with northern anchovy off California (Smith and Hewitt 1985a). Of the 2,094 Peruvian anchovy eggs produced per square meter, 67% died on the first day while off California; of the 300 northern anchovy eggs produced per m^2, 22% died on the first day. While anchovy are omnivorous in both areas, phytophagy is considered more pronounced off Peru (MacCall 1980).

Pauly (1987) found that knowledge of the rate of cannibalism appears crucial for managing the Peruvian anchovy. The rate of cannibalism on eggs is admittedly high, but it may be that the variation in the rate of cannibalism is insufficient to explain the variation in the rates of recruitment. It remains to be seen if interannual differences in the relative proportion of feeding by filtration on the one hand and biting on the other hand are sufficient to explain differences in recruitment.

The difference in conclusions regarding northern anchovy egg cannibalism between Peterman et al. (1988) for California anchovy and Pauly (1987) for the Peruvian anchovy, may be due to a simple difference in population density between the two regions, California having a much lower population density than Peru. Pauly (1987) showed the relationship between population size and egg mortality: a better relationship would be between local population density and egg mortality (Csirke 1980; MacCall 1980; Ware and Tsukayama 1981).

Egg mortality rate and adult biomass density are closely related in interregional and interannual egg production assessments (Fig. 3). The relationship is surprisingly close when one considers biomass of juvenile anchovy, the biomass of other filtering fishes, particularly sardines, and the biomass of invertebrate predators have been neglected. In Table 6, one can see that northern anchovy assessment studies off California (Stauffer and Picquelle 1981; Stauffer and Charter 1982; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986) and South Africa (Armstrong et al. 1988) differ a great deal from the assessment study reported in this paper for Peru. The median biomass density of adult anchovy was 6 g/m^2 off California between 1980 and 1985, while the median percent eggs dying each day was 16%/d. In the south Benguela Current, the mean biomass density of adult anchovy was 12 g/m^2, and the mean percentage of eggs dying per day was 22% (Armstrong et al. 1988). The median regional estimate for 1981 of biomass density of adult anchovy was 33 g/m^2 off Peru, and the egg mortality was 61% egg mortality per day. While these observations suggest cannibalism as a cause, the mortality rate of eggs may only be a consequence of generally higher populations of a wide range of other vertebrate and invertebrate predators in prime schooling fish-feeding areas.

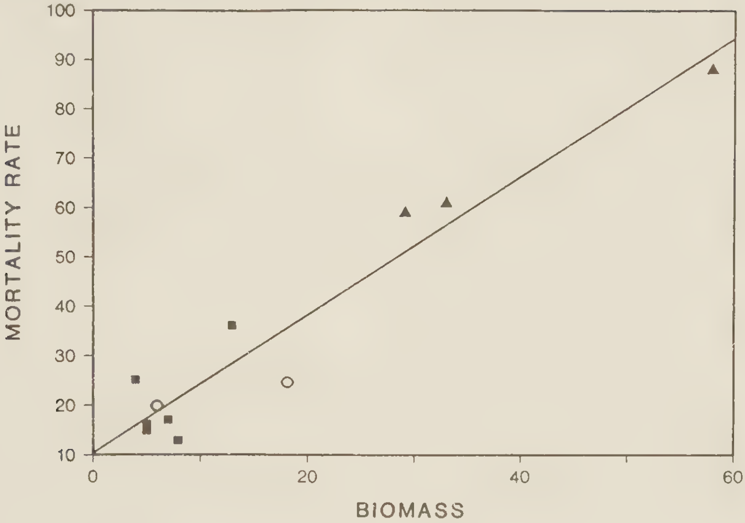

FIGURE 3.—Mortality rates in percent per day of anchovy aggs as a function of anchovy spawning biomass concentration in grams per square meter; closed triangles, Peru in nearshore regions IMAR11, IMAR21, IMAR31 (this paper); closed squares, values for the entire spawning region off California from 1980 to 1985 (Stauffer and Picquelle 1981; Stauffer and Charter 1982; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986); and, open circles, for the entire spawning region off South Africa in 1985 and 1986 (Armstrong et. al. 1988).

TABLE 6.—Anchovy egg mortality rate and adult spawning biomass concentration in the Humboldt (*Engraulis ringens*), California (*E. mordax*), and southern Benguela (*E. capensis*) currents.

Year/region	Spawning area (km^2 $\times 10^{-3}$)	Spawning biomass (tons $\times 10^{-3}$)	Biomass concentration g m^{-2}	Egg mortality % d^{-1}
Peru 8108				
IMAR11	7.9	460	58	88
IMAR21	12.9	420	33	61
IMAR31	11.2	320	29	59
CalCOFI 8003[1]	66.1	870	13	36
CalCOFI 8102[2]	77.5	635	8	13
CalCOFI 8202[3]	83.0	415	5	15
CalCOFI 8302[4]	94.7	652	7	17
CalCOFI 8402[5]	61.6	309	5	16
CalCOFI 8502[6]	132.2	522	4	25
Benguela				
1985[7]	107.1	614	6	20
1986[7]	109.8	2006	18	24

[1] Stauffer and Picquelle 1981.
[2] Stauffer and Charter 1982.
[3] Picquelle and Hewitt 1983.
[4] Picquelle and Hewitt 1984.
[5] Hewitt 1985.
[6] Bindman 1986.
[7] Armstrong et al. 1988.

CONCLUSION

MacCall (1980) stated that only 10% of the apparent control of northern anchovy recruitment off California may be due to stock size, with the vast majority of control arising from means that are independent of stock size. Lasker and MacCall (1983) concluded that the best measures of the stock recruitment curve are not sufficient domed for cannibalism to be a “major regulatory mechanism”. Also, it appears from examination of the life stages of northern anchovy (Smith 1985, table 3) moderate reproductive failures could happen at the fecundity, embryonic, larval, and juvenile prerecruit stages, but a reproductive success of great proportions would most likely arise at the embryonic and larval stages. The size of the recruited year class will accumulate the rates of early stages, and the later the prerecruits are evaluated, the more likely the reproductive success will have been established. Peterman et al. (1988) evaluated only the first 20 days of life.

For 6 successive years (included in Peterman et al. (1988)), the interannual coefficient of variation of the spawning biomass was 35% and the interannual coefficient of variation of recruitment was 104%. Only two life history parameters varied more than the spawning biomass (35%): adult density per unit area (47%) and egg mortality (38%) (Smith and Moser 1988). While cannibalism is sufficiently important as a source of egg mortality to control the size of populations like sardine and anchovy over the long term, it is unlikely that the interannual variation in rates of mortality due to cannibalism are sufficient to cause major recruitment variations. One would suspect that variability in egg mortality rate could arise from the 70% of egg mortality not due to cannibalism. Off California, Theilacker (1988) has estimated that the rate of northern anchovy egg consumption by juvenile and adult euphausiids may account for 28% of the egg mortality. Other influences on recruitment could arise from copepod predation on yolk-sac larvae (Lillellund and Lasker 1971) and predation of Pacific mackerel on juveniles (Methot 1986[6]).

To manage variable stocks like the sardine and anchovy it may be sufficient to monitor the age structure of the catch and the production and survival of the embryonic stage (Methot and Lo 1987[7]). A decrease in the number of older, highly fecund, spawning age classes will decrease effective population fecundity. In filter feeders like sardine and anchovy, cannibalism by younger age classes may lower the survival of eggs. Thus, merely by monitoring age structure and egg survival one can project when large, unusually successful year classes are possible. New techniques for monitoring juvenile abundance and growth will be required when a sardine or anchovy fishery becomes so intensive that an early recruitment prediction is necessary.

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A Method for Correcting Catches of Fish Larvae For the Size Selection of Plankton Nets

David A. Somerton and Donald R. Kobayashi

ABSTRACT: **Length distributions of fish larvae obtained with plankton nets are usually biased because large larvae avoid the net and small larvae are extruded through the meshes. Such bias is often corrected by determining the ratio between a standard net and a test net with either zero extrusion or zero avoidance. However, when avoidance of the test net with zero extrusion or when extrusion through test net with zero avoidance differs from the standard net, then the usual method of correcting for size selection results in biased estimates. For such situations, we propose a method that explicitly considers both differential extrusion and differential avoidance and that provides estimates of variance for the corrected length-frequency distributions. The method was applied to length-frequency data for the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. It was shown that a 1 m plankton net with 0.335 mm mesh dropped vertically through the water column during the day effectively samples nehu larvae only between 2.25 and 6.75 mm, roughly one-third of the total length range.**

For many aspects of larval fish ecology, accurate estimates of length distribution are imperative, yet the length distribution of larvae obtained with a plankton net is nearly always biased because large larvae avoid the net and small larvae are extruded through the meshes. Previous research on methods to correct larval catches for such size selection has focused on either extrusion (Lenarz 1972) or avoidance (Barkley 1972; Murphy and Clutter 1972), implicitly assuming that the two aspects of size selection are independent. Although this assumption seems reasonable, situations arise in which the problems of estimating extrusion and avoidance are unavoidably linked.

Nearly all empirical or analytical studies of avoidance and extrusion are based on the premise that the number of larvae captured by a plankton net (N_o) is proportional to the number originally in the path of the net (N):

$$N_o = P_c\, N\,, \tag{1}$$

where the proportionality constant (P_c) varies with larval length. P_c can be considered as the probability of capturing a larva, and this, in turn, can be considered as a product of an entry probability (P_e) and a retention probability (P_r):

$$P_c = P_e\, P_r; \tag{2}$$

where P_e is equal to 1 minus the probability of a larva avoiding the net and P_r is equal to 1 minus the probability of a larva being extruded through the meshes, given that it has entered the net.

Since an estimator for N can be obtained by combining and rearranging the above equations,

$$N = \frac{N_o}{P_e\, P_r}\,, \tag{3}$$

the problem of correcting for size selectivity is one of estimating P_e and P_r for each length interval.

To estimate P_e or P_r, catches of a standard net are usually compared with those obtained by some test net used to sample the same population of larvae. In this paper, we will refer to these comparisons as either entry or retention experiments. Assuming catches are standardized to reflect equal filtration volumes, the general form of a net comparison is

$$\frac{N_{os}}{P_{es}\, P_{rs}} = \frac{N_{oi}}{P_{ei}\, P_{ri}} = N\,, \tag{4}$$

where the second subscript refers to the standard net (s) and to the test net used in either an entry experiment ($i = e$) or a retention experiment ($i = r$). Expressed in words, Equation (4) states that the corrected catches from the standard and test nets are both unbiased estimates of the true abundance of larvae and are therefore equal.

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For an entry experiment, an appropriate test net is one that has no larval avoidance (i.e., $P_{ee} = 1.0$) over the size range of interest. After substituting this value for the entry probability and rearranging terms, Equation (4) can be expressed as

$$\frac{N_{os}}{N_{oe}} = \frac{P_{rs}}{P_{re}} P_{es} . \tag{5}$$

Likewise, for a retention experiment, an appropriate test net is one that has no larval extrusion (i.e., $P_{rr} = 1.0$). After substituting this value for the retention probability and rearranging terms, Equation (4) can be expressed as

$$\frac{N_{os}}{N_{or}} = \frac{P_{es}}{P_{er}} P_{rs} . \tag{6}$$

To simplify Equations (5) and (6) further, previous studies have assumed that either the larval retention of the test net used in an entry experiment was identical to that of the standard net (i.e., $P_{rs} = P_{re}$; Barkley 1972; Murphy and Clutter 1972) or that the larval entry into the test net used in a retention experiment was identical to that of the standard net (i.e., $P_{es} = P_{er}$; Lenarz 1972; Colton et al. 1980; Leak and Houde 1987). With these assumptions, Equations (5) and (6) become

$$\frac{N_{os}}{N_{oe}} = P_{es} , \tag{7}$$

and

$$\frac{N_{os}}{N_{or}} = P_{rs} . \tag{8}$$

In other words, entry and retention probabilities of the standard net were estimated as the ratio of the catches of the standard and test nets within each length interval.

When neither assumption can be made, the estimation procedure is complicated in two ways: First, P_{es} and P_{rs} cannot be estimated as simple ratios of the catches of the standard and test nets because they additionally depend on other unknown entry and retention probabilities. This means that P_{es} and P_{rs} cannot be estimated independently for each length interval and must instead be expressed as functional relationships of larval length and estimated simultaneously for all size intervals. Second, the equations for the entry experiment, Equation (5), and the retention experiment, Equation (6), contain both P_{es} and P_{rs}; therefore, the two probabilities are confounded and must be estimated jointly.

In this paper, a method is described for estimating the entry and retention probabilities for this more difficult situation, and this method is then applied to correct the length-frequency distribution of larval Hawaiian anchovy or nehu, *Encrasicholina purpurea*, obtained with plankton nets.

MATERIALS AND METHODS

The standard plankton net that we used to sample eggs and larvae of nehu was constructed of 0.335 mm Nitex[1] and measured 1 m in diameter and 5 m long. The net was not towed but deployed instead by our allowing it to drop vertically through the water column until it hit the bottom, then retrieved with a line attached to a choke collar surrounding the mesh approximately 15 cm from the mouth of the net.

Retention and entry experiments were conducted on 28 March 1988 within Pearl Harbor, HI. The retention experiment consisted of 10 paired net drops, in which the standard net and a test net were deployed simultaneously at one location during daylight hours when the standard net was normally used. The test net was identical to the standard net in all dimensions, but it had a smaller mesh size (0.183 mm). The entry experiment was conducted at each of three nearby (<0.5 km distance) locations and consisted of five deployments of the standard net during the day and five deployments of the same net the following night at each location. Since sampling could not be paired in this experiment, we were concerned that patchiness and horizontal movement of fish by tidal currents might alter the length distribution between day and night sampling. To reduce this, the sampling locations chosen had weak tidal currents, and in addition, sampling was partitioned between three locations rather than concentrated at one. Water depth at all sampling locations was approximately 12 m. The sample obtained from each deployment of each net was stored separately in 10% buffered formalin.

During the retention experiment, the test net appeared to become clogged with algae despite efforts to clean it between deployments. To determine whether the test net was indeed clogged and filtered less water than the standard net, we assumed filtration volume was proportional to the catch of nehu eggs and used a paired *t*-test to compare egg catches between nets. The test net caught significantly fewer eggs ($P < 0.05$); therefore, the test net was assumed to have filtered less water. To correct for the difference in filtration volume, larval catches in the test net were multiplied by the ratio of the egg catch of the standard net to that of the test net in each pair of deployments.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Nehu larvae were subsequently measured to the nearest 0.1 mm by using a video digitizing system (Optical Pattern Recognition System produced by Biosonics, Inc., Seattle, WA). For preflexion and early flexion larvae, length was measured from the snout to the end of the notochord. For larvae with fully formed tails, length was measured from the snout to the base of the caudal fin rays. The length distributions were not corrected for shrinkage due to preservation, but since all samples were maintained in preservative for about the same length of time, it is unlikely that shrinkage varied among samples.

The entry and retention probabilities were estimated by simultaneously fitting Equations (5) and (6) to the length-frequency data by using nonlinear regression, but before this could be done, three problems had to be solved. First, the entry and retention probabilities could not be estimated independently for each length interval; therefore, Equations (5) and (6) had to be modified so that the probabilities were expressed as functions of larval length. Retention probabilities were chosen to vary with length as logistic functions and thus have the form $P = 1/(1 + ae^{-bl})$, where a and b are parameters to be estimated and l is larval length (Ricker 1975). Entry probabilities, because they are decreasing functions of length, were chosen to have the form $P = 1 - (1/(1 + a\ e^{-bl}))$. After the logistic functions were substituted for the two entry probabilities (P_{es} and P_{er}) and two retention probabilities (P_{rs} and P_{re}) in Equations (5) and (6), the resulting statistical model had eight parameters.

Second, variability in the catch ratio changed with larval length, owing to the change in sample size, and necessitated the use of weighting factors in the regressions (Draper and Smith 1981). The weighting factors used were equal to $1/\mathrm{var}(N_{os}/N_{oi})$, where *var* is the variance and N_{oi} can be either N_{or} or N_{oe}. Variance of the catch ratio was approximated by using the delta method (Seber 1973):

$$\begin{aligned}\mathrm{var}(N_{os}/N_{oi}) = {} & (1/N_{oi})^2\ \mathrm{var}(N_{os}) \\ & + (N_{os}/N_{oi}^2)^2\ \mathrm{var}(N_{oi}) \\ & - 2\ (N_{os}/N_{oi}^3)\ \mathrm{cov}(N_{os},N_{oi})\ , \quad (9)\end{aligned}$$

where cov indicates covariance. The number of larvae captured in each length class (N_o) was assumed to vary as a multinomial random variable. The variance of N_o was therefore expressed as $N_{\bullet}P(1 - P)$; where N_o is either N_{os}, N_{or} or N_{oe}; $N_{\bullet}$ is the sum of N_o over all length intervals; and $P = N_o/N_{\bullet}$. Although the covariance between the catches of the standard and test nets could be estimated for the retention experiment, it could not be estimated for the entry experiment because sampling was not conducted pairwise. However, the covariance term for the retention experiment was, for all size intervals, approximately 100 times less than the sum of the two variance terms (Equation (9)). On this basis, we assumed that the covariance term was generally small and could be ignored in both the entry and retention experiments.

Third, since the catch ratios fluctuated widely and often became infinite in the larger length intervals where sample sizes were small, the length distributions were truncated prior to fitting the equations. For the entry experiment, truncation occurred at the smallest length interval with zero catch by the test net. For the retention experiment, however, this rule resulted in an extremely narrow length range because the catches obtained with the test net were zero at relatively small lengths. To circumvent this problem, the inverse of Equation (5) was fit to the data, and truncation occurred at the smallest interval with zero catch by the standard net. Weights were calculated by using Equation (9) after substituting N_{os} for N_{oi} and vice versa.

Once Equations (5) and (6) had been fit to the data, the values P_{rs}, P_{re}, P_{es}, and P_{er} were estimated by evaluating the logistic functions at each 0.5 mm length interval using the parameter estimates. P_c for the standard net was calculated for each length interval as the product of the estimates of P_{es} and P_{rs}. Length-frequency data from nehu larvae were then corrected for extrusion and avoidance by dividing each N_o by the estimated value of P_c for the appropriate length interval. To better visualize the effect of this correction, we chose N_o from a data set that was considerably larger ($N = 4{,}178$) than those used in the net comparisons because histograms of this larger data set were smoother in appearance. This larger data set comprises all larvae that we have measured to date (including those obtained in the net comparisons) and that were collected during the day by the standard net.

The variance of the estimated value of N was approximated by using bootstrapping (Efron and Gong 1983): 1) each of the four experimental length-frequency data sets was randomly subsampled with replacement to produce four new samples with the same sample sizes as the originals; 2) Equations (5) and (6) were fit to the four synthetic samples by the methods described above; 3) P_{es}, P_{er}, P_{rs}, P_{re}, and P_c were estimated for each length interval; and 4) N for each length interval was estimated by dividing the N_o from the large sample of nehu length-frequency data by the estimated value of P_c. This procedure was repeated 500 times, generating 500 independent estimates of P_c for each length. To reduce variance owing to rare but extremely large estimates of N produced when P_c was near 0, the data were trimmed by eliminating the 25 largest estimates within each length interval (5% of the sample). After data trimming, the variance was calculated among the remaining 475 independent estimates.

The variances of P_{es}, P_{er}, P_{rs}, and P_{re} were also calculated from the same 500 independent estimates (no data trimming was required). A two-sample t-test incorporating these variances was then used to test for significant differences between P_{es} and P_{er} and between P_{rs} and P_{re} within each length interval.

RESULTS AND DISCUSSION

The estimated entry probabilities for the standard net (P_{es}) decreased from 1.00 for 3 mm larvae to near 0.00 for 10 mm larvae, whereas the entry probabilities for the small mesh net (P_{er}) decreased from 0.95 for 3 mm larvae to near 0.00 for 8 mm larvae (Fig. 1). When the apparent difference in entry probabilities between the two nets was examined statistically for each 0.5 mm length interval between 2.5 and 10.75 mm, P_{er} was found to be significantly less than P_{es} (two-sample, one-tailed t-test; $P < 0.05$) for all length

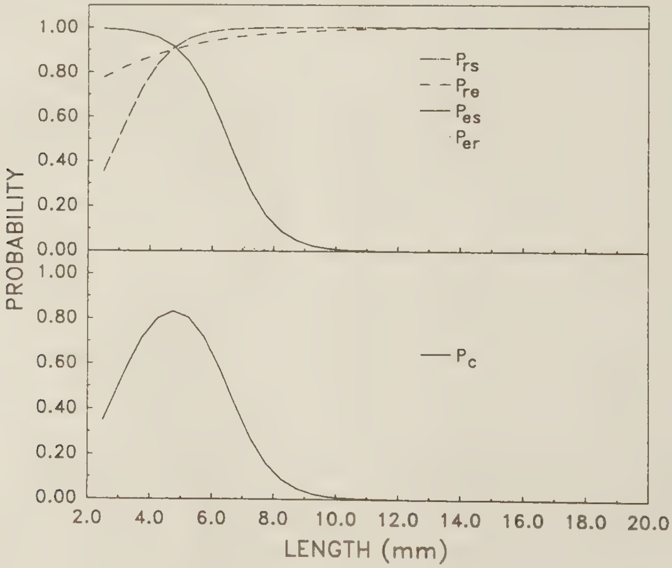

FIGURE 1.—Entry probabilities for the standard (P_{es}) and test nets (P_{er}) and retention probabilities for the standard (P_{rs}) and test nets (P_{re}) are shown by 0.5 mm length intervals (upper panel). Capture probability (P_c) for the standard net is shown by 0.5 mm length interval (lower panel).

intervals ≥4.25 and ≤6.75 mm. This result is surprising because the two nets were identical except for mesh size which, by itself, is unlikely to influence avoidance. However, the catch of nehu eggs in the test net was significantly less than in the standard net (paired *t*-test, $P < 0.05$), indicating, to the extent egg catches can be used as a measure of filtration volume, that the test net was likely clogged by abundant filamentous algae in Pearl Harbor during sampling. Such clogging not only decreased the apparent amount of water entering the test net but also may have slowed the sinking rate, allowing larvae to avoid the net more easily.

The estimated retention probabilities for the standard net (P_{rs}) during the day increased from about 0.35 for 2.5 mm larvae to nearly 1.00 for 6.0 mm larvae (Fig. 1). At night, however, the standard net appeared to have higher retention probabilities in the smallest length intervals (P_{re}; Fig. 1). When this difference was examined statistically (two-sample *t*-test), P_{re} and P_{rs} were not significantly different at $P \leq 0.05$ in any length interval, but they were significantly different at $P \leq 0.15$ within the two smallest length intervals. Although the differences between P_{re} and P_{rs} are relatively small, considering the same net and method of deployment were used during both day and night sampling, it is surprising that any differences were detected. One possible explanation is that the density of small larvae, rather than the retention probability, was higher at night. This could have occurred either because, by chance alone, the density of small larvae was higher in the patches sampled at night or because the mean density was higher as a result of eggs hatching between the day and night sampling. However, the addition of new larvae is unlikely because, at the time of year when our sampling occurred (March), nehu eggs hatch during the morning and new larvae would therefore have been equally available to both our day and night sampling (Clarke 1989). A second explanation is that the greater retention of small larvae at night is real and at least partially due to morphological changes increasing the catchability of larvae between the day and night sampling periods. Evidence for this is weak; however, Clarke (1989) reported that during March nehu larvae display considerable development of their eyes, mouth, and pectoral fins between midday and early evening of their third day of life. Development of such features might increase catchability relative to equal-sized, but undeveloped, larvae.

Regardless of the reasons, over some length ranges, $P_{rs} \neq P_{re}$ in the entry experiment and $P_{es} \neq P_{er}$ in the retention experiment; both cases are violations of the assumptions implicitly made when entry and retention probabilities are estimated as simple catch ratios (i.e., catch of standard net/catch of test net). The effect of ignoring this can be judged from plots of entry and retention probabilities estimated from simple catch ratios and estimates of P_{es} and P_{rs} using our method (Fig. 2). Entry probabilities estimated from simple catch ratios are similar to P_{es} for larvae ≥4.0 mm but are increasingly less than P_{es} at smaller lengths. This region of underestimation corresponds approximately to the length interval in which the retention of larvae differed between day and night (Fig. 1). Retention probabilities estimated from simple catch ratios are similar to P_{rs} at larval lengths <4 and >8 mm, but are considerably larger than P_{rs} at intermediate lengths. Again, this region of overestimation corresponds approximately to the length region in which avoidance differed between the standard and test nets (Fig. 1). Violation of the assumptions therefore leads to bias in estimates of entry and retention probabilities based on simple catch ratios.

The success of a net comparison, however, also depends upon the validity of several other assumptions. Foremost are the assumptions that no avoidance of the test net occurred in the entry experiment ($P_{ee} = 1.0$) and no extrusion through the test net occurred in the retention experiment ($P_{rr} = 1.0$). Violations of these assumptions lead to positive bias in the estimates of P_{es} and P_{rs}. For the entry experiment, P_{ee} was definitely higher than P_{es} over a broad range of sizes because more larvae were caught at night and a sizable fraction of the catch was larger than the largest larva caught during the day (Fig. 3). But no evidence indicates P_{ee} remained equal to 1.0 for size intervals ≤14.0 mm (the size of the largest larvae caught during the day), as is required to obtain unbiased estimates. For the retention experiment, P_{rr} was definitely higher than P_{rs} because more small larvae were captured with the test net (Fig. 3). But, again, no evidence indicates P_{rr} remained equal to 1.0 for size intervals ≥2.00 mm, the smallest size category.

Still another assumption is that, in each of the two experiments, the standard and test nets both sampled the same population of larvae. For the retention experiment, the assumption is certainly valid because the two nets were deployed

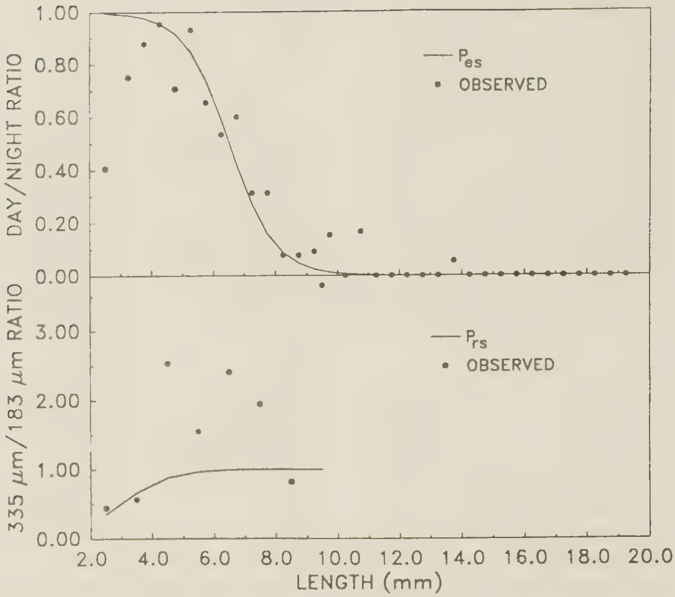

FIGURE 2.—Estimated values of P_{es} and the day to night catch ratio by 0.5 mm length intervals obtained in the avoidance experiment (upper panel). Estimates of P_{rs} and the 0.335 mm standard net to the 0.183 mm test net catch ratio by 1.0 mm length intervals obtained in the extrusion experiment (lower panel).

simultaneously from a small boat. For the entry experiment, however, deployment of one of the nets occurred approximately 10 hours after the other, and any patchiness in the larval distribution coupled with advective movement could have substantially altered the characteristics of the population sampled. We attempted to minimize this problem by increasing the sample size, relative to the retention experiment, and by partitioning the sampling among three locations rather than by concentrating it at one. Sampling variability, however, may still have been responsible for some of the differences between the day and night size distributions. This problem has been encountered in other studies using day and night comparisons to estimate entry probabilities (Murphy and Clutter 1972), and the only effective solution is increased sample sizes.

Since the method of estimating entry and retention probabilities proposed here requires more effort than that using simple catch ratios, it is important to determine at the outset whether the assumptions that $P_{rs} = P_{re}$ and $P_{es} = P_{er}$ have been violated so that the appropriate method of analysis can be chosen. Some indication of the validity of these assumptions can be obtained by examining plots of catch ratios as a function of larval length (Fig. 2). Two cases are evident in our data. First, if the assumptions are met, catch ratio should be a monotonically increasing or decreasing function of larval length because extrusion and avoidance are monotonic functions of larval length. This is not true in the avoidance experiment where the catch ratios increased for lengths $\leq$4 mm and decreased thereafter. Second, if the assumptions are met, catch ratios cannot be >1.0, because, except by chance alone, catch in the standard net is less than the catch in the test net. This is not true for the extrusion experiment where the catch ratios in some length intervals are >2.0. If either of these conditions are evident in plots of catch ratios, the method of estimating entry and retention probabilities proposed here is preferable to simple catch ratios.

Although we considered the problem in which both $P_{rs} \neq P_{re}$ and $P_{es} \neq P_{er}$, this is the most general of several related problems that could be approached with slight variations in our methodology. One example occurs when either $P_{rs} \neq P_{re}$ or $P_{es} \neq P_{er}$ but not both. In this case, either

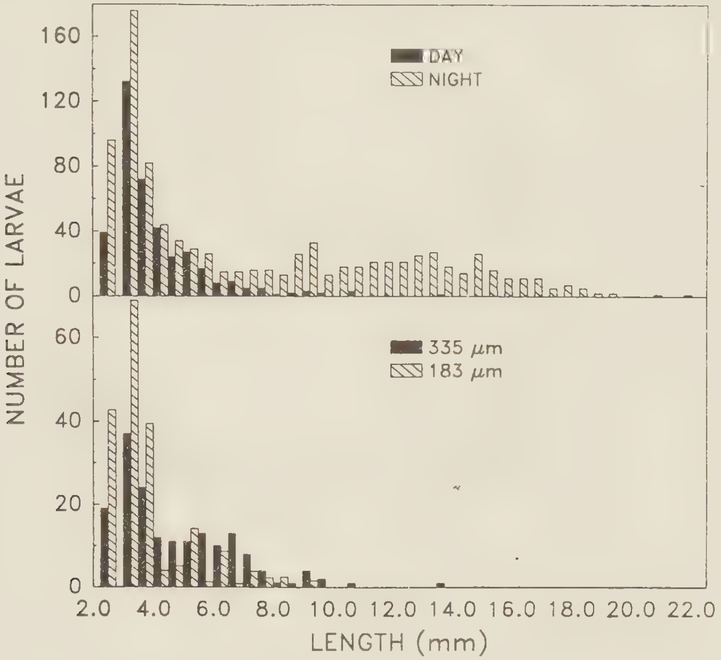

FIGURE 3.—The number of larvae by 0.5 mm length intervals captured in Pearl Harbor, HI, in March 1988. The entry experiment (upper panel) used a 0.335 mm standard mesh net during the day and night. The retention experiment (lower panel) used both a 0.183 mm mesh test net and a 0.335 mm standard mesh net during the day.

Equation (5) or (6) could be simplified by deleting either P_{rs}/P_{re} or P_{es}/P_{er}, but parameter estimation would still require a simultaneous fit of the two equations to the catch ratios. A second example occurs when only an entry experiment or retention experiment is conducted and the appropriate assumption is violated. In this case, the entry and retention probabilities still must be expressed as functions of larval length, thus requiring that nonlinear regression be used to fit either Equation (5) or (6) to the catch ratios.

The efficacy of the standard net at sampling nehu larvae can be judged in two ways. First, it can be judged by the length range sampled with a P_c = 1.0; that is, the range that requires no correction for extrusion and avoidance. For the standard net, P_c reaches a maximum of 0.86 at 4.25 mm and remains above 0.75 only over the interval 3.75–5.50 mm (Fig. 1). In other words, no interval within the larval length range of nehu (2.5–25.0 mm) is sampled completely with the standard net.

A second way of judging the efficacy of the standard net is by the length range than can be corrected, with sufficient precision, for extrusion and avoidance. The effect of correcting a large sample of nehu length frequencies for extrusion and avoidance can be seen in the frequency distributions before and after N_o was divided by the estimated value of P_c (Fig. 4). The precision of this correction can be gauged from the estimates of the variance of N (Fig. 5). Note that variance increases gradually with length until 6.75 mm and, thereafter, increases at a greatly accelerated rate. If 6.75 mm is chosen as the upper bound on the length interval within which the estimated numbers are considered sufficiently precise, then only one-third of the larval length range could be corrected to reflect the true length distribution. Thus, judging from either perspective, the standard net is a relatively ineffective tool for sampling nehu larvae.

Variance of the corrected length-frequency distribution was used above to define some length range that can be corrected for extrusion and avoidance with sufficient precision, but estimates of variance have other important uses,

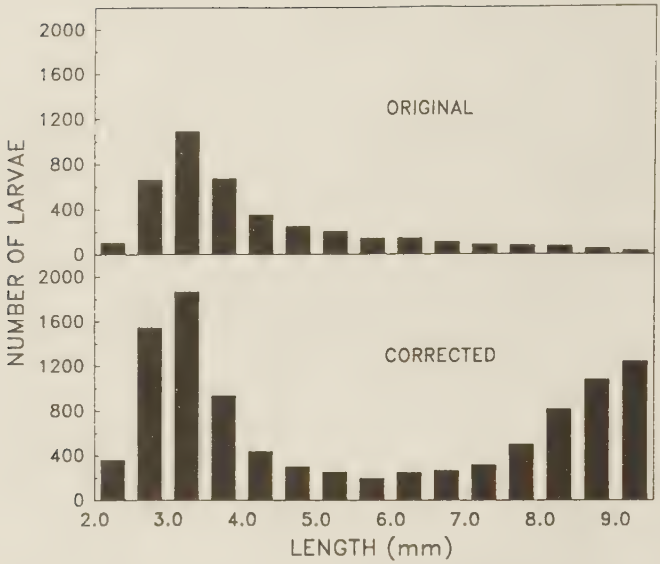

FIGURE 4.—Length distribution of nehu larvae by 0.5 mm intervals before correction for extrusion and avoidance (upper panel) and after correction (lower panel).

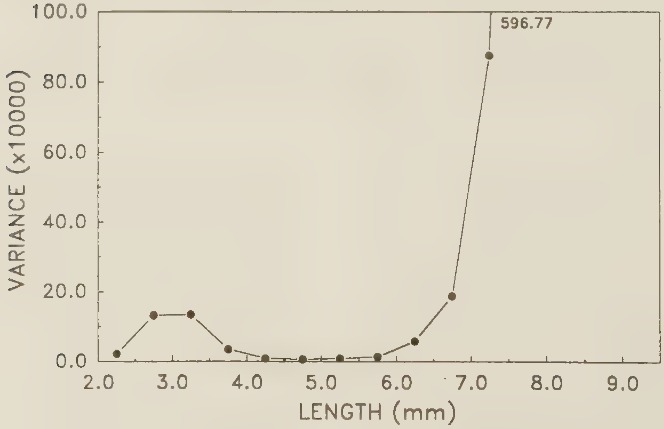

FIGURE 5.—Bootstrap estimate of variance of the corrected number of larvae by 0.5 mm length intervals.

especially when the corrected length-frequency distributions will be subsequently used to estimate mortality rates. Whether mortality is estimated by using methods that require converting length-frequency distributions to age-frequency distributions (Leak and Houde 1987) or by using some form of length-based method (Wetherall et al. 1987), precision of the mortality estimates will depend on the precision of corrected length-frequency distributions. Thus, procedures used to estimate mortality from larval length-frequency distributions should include weighting factors that incorporate the size-specific variances of the corrected length-frequency distributions.

Most of the problems associated with violations in the assumptions $P_{rs} = P_{re}$ and $P_{es} = P_{er}$ could be eliminated with proper attention to the design of the entry and retention experiments. When these assumptions are violated, unbiased estimates of entry and retention probabilities can sometimes be obtained by restricting the analysis to either large or small larvae to ensure that avoidance and extrusion do not simultaneously influence the size distribution. If the size range of interest must be as broad as possible, however, then the methods described in this paper can be used to correct for differential extrusion and avoidance and unbiased length-frequency distributions can thereby be obtained.

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INTEGRATION OF JAPANESE AND UNITED STATES SABLEFISH MARKETS

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ABSTRACT

As United States sablefish production becomes more tightly interwoven with Japanese markets, the U.S. sablefish fleet could become more vulnerable to changes in Japanese market conditions and government policies, and U.S. policies would have to be formulated with an eye on Japanese conditions. If U.S. ex-vessel and Japanese markets are integrated by prices, then price information transmitted from the Japanese market affects the behavior of the U.S. markets, while in turn, if the markets are not price integrated, U.S. market behavior is independent of price movements in Japan. To assess this likely market integration, this paper examines the price integration of the Pacific coast and Alaska's fixed gear ex-vessel markets and the Tokyo central wholesale market over 1981–1986. The Pacific coast market is found to be segmented from the Tokyo market while a form of price integration exists between the Tokyo and Alaska markets. The paper concludes with a number of implications for policies in both the United States and Japan.

Following the Manguson Fishery Conservation and Management Act (MFCMA) of 1977, United States fishermen have been given an opportunity to replace foreign harvesters of several species as the first link in a chain of supply for some foreign markets. In few fisheries have the results of this industry domestication been more strongly demonstrated than in those for Pacific sablefish. As the Japanese witnessd their harvest in U.S. territorial waters fall from 25,000 to 50,000 thousand metric ton (t) range in the mid-70's to negligible amounts in recent years, U.S. producers expanded their sablefish operations, thereby facilitating greater U.S. exports. Throughout much of the early 1980's, these increases in U.S. exports were accompanied by continued reductions in Japanese harvests.

These factors have combined to increase the ex-vessel sablefish revenue received by Pacific coast and Alaska groundfish fishermen to a level second only to that for Alaska pollock. In contrast to pollock, which is currently harvested predominantly by joint venture operations, sablefish is almost exclusively domestically harvested and processed. The dramatic increase in U.S. production and revenues had coincided with an increase in U.S. sablefish exports to Japan from just 340 t in 1981 to roughly 12,000 t in 1986.

The growing reliance of Japanese sablefish markets on U.S. exports concomitant with an expanding U.S. sablefish fleet suggests the possibility of a growing integration of the Japanese and U.S. ex-vessel sablefish markets. To the extent that U.S. production becomes more tightly interwoven with Japanese markets, the U.S. sablefish fleet will become more vulnerable to changes in Japanese market conditions. Changes in Japanese prices or the exchange rate have a much greater potential for impacting U.S. fishermen today than even 5 or 10 years ago. This possibly increasing integration of U.S. ex-vessel and Japanese sablefish markets by both price and commodity flows and the increased economic dependence on the U.S. export of sablefish for both societies underscores the need for a better understanding of the manner in which these markets are integrated.

This paper empirically examines the integration by prices of U.S. and Japanese sablefish markets over the time period 1981–86. We consider the Tokyo central wholesale (Tsukiji) market and the U.S. ex-vessel markets in Alaska and along the Pacific coast. Because quite a sizable amount of the domestically caught sablefish is retained in the United States, consideration of U.S. markets at some level beyond the ex-vessel might seem desireable, but we restrict our attention to the ex-vessel level because of data availability. We further restrict

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our analysis to the pot and longline, or fixed gear, sector of the fleet, because these vessels produce the higher quality sablefish desired by Japanese consumers.

We consider Tokyo the central wholesale market, because it is playing an increasingly dominant role in the handling of sablefish in Japan. Before the imposition of harvest restrictions, when the Japanese fishing fleet was responsible for providing most of the domestically consumed sablefish, the centralized market in Tokyo played a less important role in the distribution of sablefish; it may have handled less than 50% of that consumed. As Japan was forced to rely increasingly on imports of sablefish, the clearinghouse in Tokyo has become more prominent by providing a conduit for the imported product. Throughout most of the 1980's, the Tokyo market has generally handled 60–70% of the sablefish sold in Japan.

MARKET INTEGRATION AND PRICE ANALYSIS

This section defines market integration and presents the formal models used to empirically assess the structure of any price integration which may exist.

Market Integration

Markets integrated by prices are those markets in which prices do not behave independently. In market economies, market information to the different participating economic agents is largely transmitted by prices, so that an understanding of the manner in which markets are integrated by prices can contribute to the general process of policy formulation. Markets may be integrated by prices to different degrees and along some dimensions but not others. Geographical links or interregional trade are among the most important. Two major issues of these spatial price linkages have been most frequently examined: whether or not markets are integrated by prices, and if so, the extent and nature of this integration.

Regression analysis is the preferred method of assessing market integration. This procedure implicitly assumes that prices of commodities in spatially dispersed markets can independently move in a nonintegrated market system. Changes in weather patterns or government policies affecting the quantity and price of a commodity in a market should not have an impact on prices in other markets when the market system is not integrated by the price mechanism. Price movements across markets would be fundamentally independent, and price movements within markets would reflect local responses to local conditions.

Dynamic Spatial Price Differentials

Ravallion (1986) recently proposed a dynamic model of spatial price differentials from a central market to local markets for a tradeable good. Ravallion's model permits each local price series to have its own dynamic structure, allows for any correlated local seasonality or other characteristics, and provides for an interlinkage with other local markets. Moreover, the alternative hypotheses of integration of markets by price and market segmentation are encompassed within a more general model, thereby allowing for nested statistical testing. Finally, Ravallion's dynamic model distinguishes between the concepts of instantaneous market integration and the less restrictive idea of integration as a long-run target of the short-run dynamic adjustment process. Thus, while short-run adjustment could be statistically rejected by the data, so that trade does not immediately adjust to spatial price differentials, it is still possible to determine if there is any long-run tendency toward market integration.

Ravallion (1986) proposed the following econometric model of a T-period series of prices for N regions:

$$P_{it} = \sum_{j=1}^{J} a_{ij} P_{it-j} + \sum_{j=0}^{J} b_{ij} P_{1t-j} + c_i X_{it} + e_{it}, \quad i = 2, \ldots, N, \qquad (1)$$

where market 1 is the central market (here Tokyo), X_i ($i = 1, 2, \ldots, N$) is a matrix of nonprice influences on local markets, the e_{it}'s are appropriate error processes, J is the number of time periods to be lagged, and the a's, b's, and c's are parameters to be estimated.

Several hypotheses about interregional trade and market integration can be formulated as linear parameter restrictions on Equation (1) and tested by F-tests (Ravallion 1986):

Market Segmentation

The null hypothesis of local market segmentation states that changes in the central market prices will have no effect, immediate or lagged, on prices in the ith local market. Market i could be called segmented if

$$b_{ij} = 0, \quad j = 0,1,2,\ldots,J, \tag{2}$$

which can be determined by imposing the parameter restriction of Equation (2) on Equation (1), and testing this restricted model against the unrestricted model of Equation (1) with an F-test. Nonrejection of the linear restrictions or null hypothesis indicates that the price in local market i depends only on its own lagged values and local market characteristics.

Short-Run Market Integration

A price change in the central market will be immediately and fully passed on to the ith local market price if

$$b_{i0} = 1. \tag{3}$$

This hypothesis, in addition, requires that there be no lagged effects on prices in the future:

$$a_{ij} = b_{ij} = 0, \quad j = 1,2,\ldots,J. \tag{4}$$

If both Equations (3) and (4) are accepted as parameter restrictions, then market i is integrated with the central market within one time period.

A weaker form of short-run market integration will also be tested, in which the lagged effects need only vanish on average:

$$\sum_{j=1}^{J} a_{ij} + \sum_{j=1}^{J} b_{ij} = 0. \tag{5}$$

An additional indicator of short-run market integration occurs if $b_{i0} = 1$, but Equation (4) or (5) do not hold (Heytens 1986). In this case, short-run market integration cannot be accepted, yet economic forces causing central market price changes are generally being reflected in the local price level. A form of integration is occurring, even though the central and local markets are not being fully linked in the short run; that is, changes in the price margin between the central and local markets are not being fully passed on.

Absence of Local Market Characteristics

This hypothesis assumes that

$$c_i = 0, \tag{6}$$

where c_i is a vector if there is more than one local market characteristic. Testing this hypothesis is of interest when local prices are suspected to have different seasonality than the central market. In this case, X_{it} can be defined as a matrix of dummy variables.

Long-Run Market Integration

A long-run equilibrium is one in which market prices are constant over time, undisturbed by any local stochastic effects. Thus, when $P_{it} = P_i^*, j = 2,\ldots,n$, $P_{1t} = P_1^*$, and $e_{it} = 0$ for all t, Equation (2) takes the form

$$P_i^* = \frac{P_1^* \sum_{j=0}^{J} b_{ij} + X_{it}c_i}{1 - \sum_{j=1}^{J} a_{ij}}. \tag{7}$$

Long-run market integration now requires that

$$\sum_{j=1}^{J} a_{ij} + \sum_{j=0}^{J} b_{ij} = 1. \tag{8}$$

If this linear parameter restriction is not rejected by an F-test, then the short-run process of price adjustment described by the model is consistent with an equilibrium in which a unit increase in the central market price is fully passed on in local market prices. Markets where previous central market prices and past spatial price differentials are the primary determinants of local prices (rather than previous local prices) are well connected in the sense that supply and demand conditions in the central market are communicated effectively to local markets. In the long run, the central market influences local market prices irrespective of previous local conditions, even though traders may fail to connect the two markets through commodity flows in the short run (cf Timmer 1974). Acceptance of the short-run restrictions implies long-run market integration, but the reverse is not necessarily true.

If the linear restriction for long-run market integration is not rejected, then more efficient estimates of the remaining parameters and more powerful statistical tests are possible if the model is reestimated with long-run market integration imposed. Equation (1) under long-run integration can be written in the following equivalent form (Ravallion 1986):

$$\begin{aligned} P_{it} - P_{it-1} = {} & (a_{it} - 1)(P_{it-1} - P_{1t-1}) + \sum_{j=2}^{J} a_{ij}(P_{it-j} - P_{1t-j}) \\ & + b_{10}(P_{1t} - P_{1t-1}) + \sum_{j=1}^{J-1} (b_{10} - 1 - \sum_{k=1}^{J} a_{ik} + b_{ik}) \\ & \times (P_{1t-j} - P_{1t-j-1}) + c_i X_{it} + e_{it}. \end{aligned} \tag{9}$$

Changes in local market prices, $P_{it} - P_{it-1}$, are then attributable to changes in central market prices and past spatial price differentials between local and central market prices. The latter variables allow for the possibility that the markets are not observed in an integrated equilibrium at a given time period, so that there is feedback from prior disequilibria.

Ravallion (1986) proposed the following sequence of nested F-tests for the different null hypotheses. First, test for long-run integration. If long-run market integration is not rejected, then it should be imposed on the model with subsequent tests based on a restricted form such as Equation (9). If the null hypothesis of long-run market integration is rejected, then short-run market integration and market segmentation are tested.

Specification Issues

Central and local market prices in Equation (1) might be simultaneously formed. This possibility leads to a simultaneous equation problem, so that parameter estimates could be biased and inconsistent. Ravallion (1986) noted that the simultaneity in the system can be easily dealt with by using an appropriate instrumental variables estimator. This paper uses the two-stage least squares estimate of Equation (1) formed by replacing P_{1t} with its predicted values from the reduced form equation obtained from a regression of P_{1t} against its own values lagged one period, the values of prices in all local markets lagged one period, all dummy variables, and the time trend variable.

Several nonprice influences (X_{it}) are possible. First, the influence of seasonality is accounted for by quarterly dummy variables for winter, spring, summer, and fall. Second, the possibility of long-term effects from increasing U.S. exports coupled with continued reductions in Japanese harvest are captured by a linear time trend. Third, a dummy variable for the years 1984–86 is included to capture any effects from the reduction of Japanese sablefish catch within the U.S. 200 mile zone and concomitant increase in U.S. harvests and exports of sablefish that experienced an important increase beginning in 1984 (Hastie 1988).

Lagged Effects

Any lagged effects in the model are likely to arise from sluggishness in price adjustment, delays in transportation, cold storagé inventory holdings, and expectations formation under price uncertainty (Ravallion 1986). A maximum lag of six months was chosen. This relatively long lag length allows for Tokyo's fall prices to influence Alaska's spring prices and ex-vessel markets after Alaska harvesting has tapered off over the winter months.

A 6 mo lag length also accommodates the effects of commodity flows from the Alaska's spring harvests on price formation in the Tokyo market. The peak Alaska harvests occur in late spring and early summer. The major Tokyo wholesale purchases (approximately 65% of the year's total) are concentrated from late May through October. After these purchases, cold storage inventories become particularly important in order to accommodate the major Japanese consumption, which takes place in the fall and winter months. Thus, the major inventory holdings in the marketing chain occur at a higher level than that which our study examines and should not directly affect the model.[3]

U.S. inventory holdings and transportation lags make only a minor contribution to price formation. Sablefish are shipped frozen. Cold storage holdings prior to export are relatively small and declining in importance. Beginning in 1984, these inventory holdings were generally 15% of the exports. Before 1984, cold storage holdings formed a greater proportion of exports, because exports were substantially more limited in quantity. Shipping lags are somewhat seasonal, and while no specific information is available, shipments certainly require only a relatively limited time.

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[3] While multicollinearity from current price and six lagged prices could present a problem in estimates and tests of significance for individual regression coefficients, the hypothesis tests in this paper are for the joint effects, requiring tests on the joint confidence region, so that multicollinearity presents far less of problem than it ostensibly might appear.

Asymmetric Pricing and Price Transmission

When any form of full short-run market integration is absent, price changes in the market of origin are not immediately and fully passed on to the local markets within one time period. Yet, while the central and local markets may not be fully linked by prices in the short run, if markets are not segmented, a weaker form of short-run market integration may still be taking place. Moreover, the short-run response to rising prices emanating from the central market can differ from the response to price declines. This price stickiness produces asymmetric local market price responses to central market price changes.

While the Ravallion market model does not formally incorporate these forms of market integration—incomplete short-run market integration with asymmetric pricing, a modified Wolfram (1971) framework developed by Young (1980) and Ward (1982) does offer a formal model of price formation for examining this possible form of short-run market integration. The modified Wolfram framework presented in Ward uses a finite distributed lag function:

$$P_{it} = a_{0t} + \sum_{j=1}^{J} [b_j'(P_{1t-j+1} - P_{10}) + (b_j'' - b_j')\, P_{1t-j+1}''] + e_t. \qquad (10)$$

where P_{10} indicates the central market price in the initial time period and where

$$P_{1t}'' = (P_{1t-i} - P_{1t-i-1})\, Z_{t-1}''. \qquad (11)$$

where $Z_{t-i}'' = 1$ if $P_{1t-1} < P_{1t-i-1}$.

$= 0$ otherwise.

The estimate of $(b_j'' - b_j')$ provides a direct test of the asymmetric condition, where b_j' measures the response to a rising price P_1 and b_j'' relates to a declining price P_1.

Polynomial distributed lags can be substitited into Equation (11) to provide structure, thereby reducing multicollinearity and conserving degrees of freedom. For the case of a second-order polynomial,

$$b_j' = c_0 + c_1 j + c_2 j^2$$

$$\text{and } b_j'' - b_j = d'_0 + d_1 j + d_2 j^2, \qquad (12)$$

where the c's and d's are parameters to be econometrically estimated. The values and standard errors of the b's can then be recovered from these estimates of the c's and d's. Significance tests on d_0, d_1, and d_2 as a group (a linear restriction on Equation (10)) provide direct tests of asymmetric price linkages.

DATA

Average monthly market price data for the Tokyo central wholesale market during 1981–86 were obtained from the Tokyo Central Wholesale Market Yearbook. These are implicit prices formed by dividing monthly total revenues by comparable quantities. Most of the sablefish sold in this market are not a homogenous commodity, so that movements of these average sablefish prices may reflect changes in the composition of the product form and quality. However, because we were only able to obtain simple (unweighted) arithmetic average prices formed by linear aggregation, we were forced to assume that different product forms and grades are perfect substitutes for each other. The data are in raw, unseasonalized form, without any prior seasonal adjustments or smoothing (which would otherwise confound the distributed lag relationships).[4]

Alaska and Pacific coast ex-vessel prices tend to be competitively formed. Seattle dominates as the port of export. Many of the prices received by Alaska vessels are formed in a Seattle auction, in which roughly 10–12 processors or brokers bid after the auction has received a call from an Alaska vessel reporting its catch information. Some ex-vessel prices in Alaska and the Pacific coast are directly formed when a vessel lands its catch at a processor.

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[4] Because these prices are average implicit prices, they may not be equilibrium prices. Spot prices are available, but a problem with spot prices is that the price of the time and day sampled may not be indicative of the entire month. Also, while spot prices are available for different size classes, proportions in the market mix are unavailable.

Formation of fixed prices and informal contracting occur between some processors and harvesters, but flexibility nonetheless exists in the fixed price negotiated prior to harvesting so that stochastic fluctuations in the size, quality, and composition of landings are accommodated. While wholesalers can be strung out along the coast, seemingly in a strong position to offer noncompetitive prices to vessels, competition is nonetheless stronger than initially appears among wholesalers and processors, and harvesters always have the option to land in different ports if they feel that prices are monopsonistic. In Alaska, approximately 5-7 processors handle the bulk of Alaska's products, although there are at least 50 processors in total. Complete Alaska price data were only available from 1984 through 1986.

Japanese prices were adjusted for inflation by the use of the Japanese Consumer Price Index. Japanese prices were converted to U.S. dollars after adjusting for the yen-dollar exchange rate. Japanese prices were further converted from kilograms to pounds. U.S. prices were adjusted for inflation by the GNP implicit price deflator. Japanese prices are for eastern dressed weights and U.S. prices correspond to round weight, but the empirical results should be unaffected because of a constant adjustment rate between the two product forms.

EMPIRICAL RESULTS

Figure 1 depicts the Tokyo wholesale and the Alaska and Pacific coast ex-vessel sablefish prices by month over the time periods 1984-86 and 1981-86, respectively. All prices are in constant dollars per pound, although as noted above, the Tokyo prices correspond to eastern dressed weight and the U.S. prices correspond to round weight. The figure indicates that the Tokyo wholesale prices are generally more stable than the ex-vessel prices. The

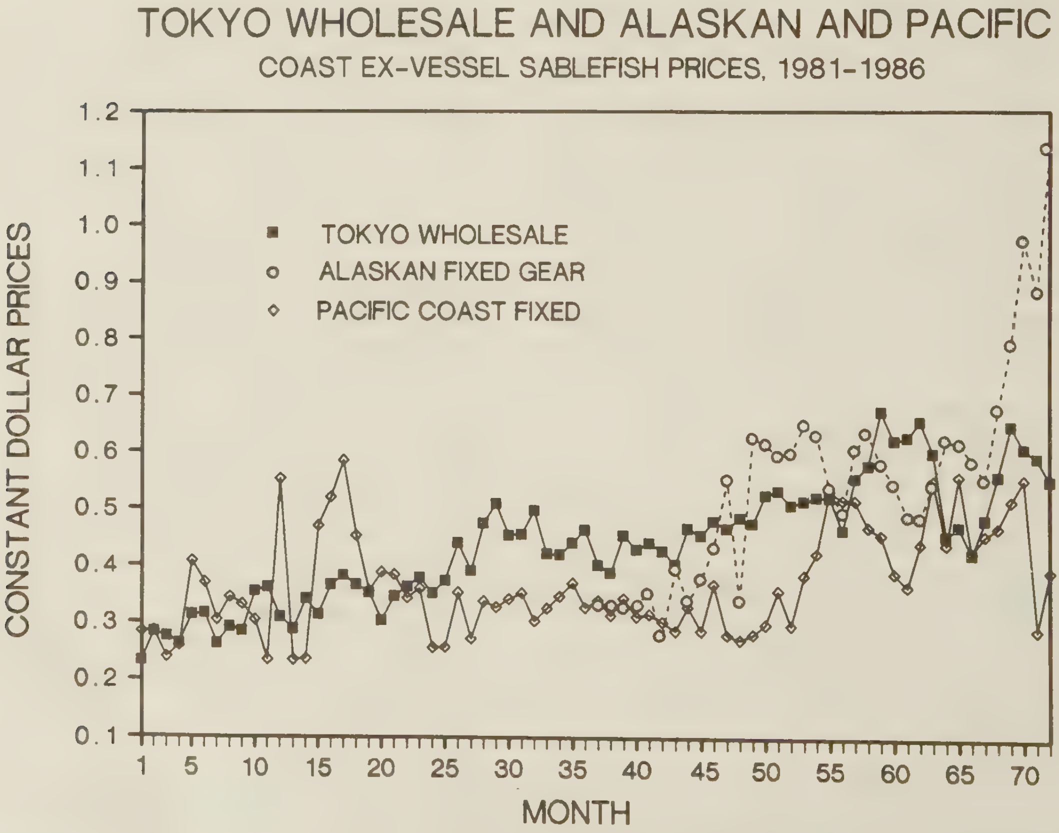

FIGURE 1.—Tokyo wholesale and Alaska and Pacific coast ex-vessel sablefish prices.

Pacific coast ex-vessel prices are also generally lower than the Alaska ex-vessel prices, perhaps reflecting a faster growth rate in market demand for Alaska's fish. An upward trend also exists for all prices. Because the Tokyo prices correspond to eastern dressed weight and correspond to a higher market level, the Tokyo prices can be generally expected to lie above the ex-vessel prices. Interestingly, this relationship only begins some time in 1983, perhaps reflecting the increasing importance of the Tokyo wholesale market as a clearinghouse for the increased imports from the United States and the sharp drop in Japanese harvests that began about this time (so that Tokyo prices now include additional transport, handling, and other market costs). Finally and most importantly, because no simple, direct, one-to-one relationship appears to exist between the Tokyo and U.S. prices, regression analysis can make an essential contribution to understanding the nature of the market integration.

To apply the Ravallion model, we specified the Tokyo wholesale market as the central market and the Pacific coast and Alaska ex-vessel fixed gear markets as the local markets.[5] The unrestricted model given by Equation (1) for six lagged periods ($J = 6$) was estimated by two-stage least squares. The autocorrelation and partial autocorrelation plots for the residuals were reasonably flat for both local markets, indicating the serial correlation does not present a problem. All statistical tests were F-tests for linear restrictions, which were all evaluated at a 5% level of significance. The results from these F-tests are reported in Table 1.

The importance of the local market characteristics was first examined. As indicated in Table 1, the null hypothesis that seasonal dummy variables for Alaska were not important was not rejected at 5%. Also, the linear trend variable was excluded because it did not contribute to the overall explanatory power of the Alaska model. The 1984 dummy variable was omitted from the Alaska model because 1984 was the first year that the Alaska's price series was used in the analysis. The seasonal dummy variables did not contribute in a statistically significant way to the unrestricted model for the Pacific coast, so that the quarterly dummy variables were not included in further regressions. The 1984 dummy variable and linear time trend did not contribute to the overall explanatory power of the unrestricted model for the Pacific coast when taken as a group (but not individually). The linear time trend for the Pacific coast was nonetheless retained in the model because of the clear upward trend in real prices exhibited by the data. The final version of the unrestricted model given in Equation (1) does not have any local market characteristics for Alaska, and only includes a linear time trend for the Pacific coast. The regression results for the final versions of the unrestricted model are reported in Table 2. These final versions of the unrestricted model were then used for the hypothesis tests on the form of market integration.

TABLE 1.—Hypothesis tests for the integration of Japanese, Pacific coast, and Alaska sablefish markets. Distributions of F-test statistics given in parentheses of form (numerator degrees of freedom, denominator degrees of freedom).

Null hypothesis	Local market	
	Pacific coast	Alaska
No local seasonality	0.458* (4,47)	3.309 (4,17)
No local time trend and 1984 dummy	1.429* (2,51)	
No local time trend		0.034* (1,22)
Long-run integration	2.870* (1,52)	0.023* (1,23)
Short-run integration		4.230 (12,24)
Short-run integration (weak form)		4.012 (2,24)
Short-run integration (weakest form)		6.621 (1,24)
Market segmentation	0.826* (6,52)	

NOTES: The unrestricted model is Equation (1) for $J = 6$ estimated using two-stage least squares. The table gives F-tests of the linear restrictions on the model implied by each null hypothesis. Short-run integration tests conditional upon maintained hypothesis of long-run integration as given in Equation (9).

* indicates nonrejection of null hypothesis at 5% level of significance.

The next null hypothesis which was tested was that of long-run market integration for Alaska. As indicated in Table 1, it was not rejected at a 5% level of significance. In order to obtain more efficient estimates of the parameters and more powerful statistical tests for the short-run market integration hypothesis test for Alaska, the model was respecified with long-run integration imposed as in Equation (9) and all subsequent tests conducted against this restricted form. (The regression results are available from the authors upon request.) All three

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[5] Within-sample, bivariate direct Granger causality tests (see Squires 1986 for a discussion) were first applied to verify if Tokyo is indeed the source of price formulation in the U.S. markets, or whether prices are simultaneously determined between Tokyo and the local markets, or whether price linkages even exist at all. The null hypotheses that prices were first formed in either the Alaska or Pacific coast ex-vessel fixed gear markets were rejected at a 5% level of significance in both instances. The null hypothesis that sablefish prices first formed in the Tokyo wholesale market lead the Pacific coast ex-vessel fixed gear sablefish prices was also rejected, thereby suggesting market segmentation. The null hypothesis that Tokyo prices lead Alaska ex-vessel fixed gear prices was not rejected, indicating some form of sablefish market integration with price leadership most likely coming from Tokyo.

TABLE 2.—Parameter estimates of dynamic model of spatial price differentials for Alaska and Pacific coast fixed gear ex-vessel and Tokyo wholesale sablefish markets. [*t* − *j*] denotes current time period less *j* time periods. Standard deviations in parentheses.

	Parameter estimates	
Variable	Alaska	Pacific coast
Time trend		0.131E-4 (0.087E-5)
Ex-vessel price [t − 1]	0.565* (0.272)	0.300* (0.149)
Ex-vessel price [t − 2]	0.381 (0.225)	0.101 (0.157)
Ex-vessel price [t − 3]	0.237 (0.235)	0.130 (0.164)
Ex-vessel price [t − 4]	0.035 (0.227)	0.345 (0.169)
Ex-vessel price [t − 5]	−0.044 (0.253)	0.180 (0.163)
Ex-vessel price [t − 6]	−0.269 (0.240)	−0.154 (0.149)
Tokyo price current	−0.593 (0.673)	−0.268 (0.438)
Tokyo price [t − 1]	0.568 (0.698)	0.255 (0.440)
Tokyo price [t − 2]	0.249 (0.361)	0.080 (0.322)
Tokyo price [t − 3]	0.237 (0.381)	−0.406 (0.314)
Tokyo price]t − 4]	−1.090* (0.359)	0.258 (0.325)
Tokyo price [t − 5]	0.723 (0.422)	−0.037 (0.320)
Tokyo price [t − 6]	−0.055 (0.275)	0.288 (0.288)

NOTE: Two-stage least squares estimates of final version of unrestricted model given by Equation (1).

* denotes statistically significant at 5%.

forms of short-run market integration were rejected for Alaska at a 5% level of significance, as indicated in Table 1.

The null hypothesis of long-run market integration was not rejected for the Pacific coast at a 5% level of significance, as reported in Table 1. However, given that this nonrejection was only marginal, the evidence was only weak for long-run integration. The alternative null hypothesis of market segmentation for the Pacific coast was therefore tested and decisively not rejected; market segmentation is the most likely market relationship.[6]

To summarize, the Tokyo wholesale and Pacific coast ex-vessel fixed gear sablefish markets are likely to be segmented over the period 1981–86. Changes in the Tokyo wholesale market prices will have no effect, immediate or lagged, on the Pacific coast market. Instead, the local market price depends only upon its own lagged values and local market conditions. Pacific coast fixed gear ex-vessel sablefish markets operate independently of the Tokyo central wholesale market. Should the expansion of sablefish export markets be considered important, then the general lack of communication of prices and other market information should be targeted for improvement.

The Tokyo wholesale and Alaska fixed gear ex-vessel sablefish markets are well integrated by prices in the sense of a long-run tendency in the short-run adjustment process. Changes in Alaska ex-vessel sablefish prices can be attributed to changes in Tokyo wholesale prices and past spatial price differentials between the Tokyo and Alaska markets. Supply and demand conditions in the Tokyo central wholesale market are communicated effectively to the Alaska ex-vessel market and influence prices there irrespective of previous local conditions. In fact, previous local prices and localized market conditions contribute little to current Alaska ex-vessel prices. These two markets are well integrated by prices in this manner, although traders may fail to connect the two markets through commodity flows in the short run, particularly during the winter months.

The absence of any form of full short-run market integration for Alaska suggests that a price change in the Tokyo wholesale market is not immediately and fully passed on to the Alaska fixed gear ex-vessel market within one month. Given the important reduction in Alaska fishing during the winter months and the dispersed and often geographically isolated nature of harvesters, processors, and brokers, this result is not surprising. Yet, while the two markets are not fully linked by prices in the short run (one month), a weaker form of short-run market integration may still be taking place due to the economic forces causing Tokyo wholesale market price changes generally to be reflected in the Alaska fixed gear ex-vessel price level.

To examine one possible form of incomplete short-run integration by price between the Alaska and Tokyo markets, the modified Wolfram model was applied. This approach allows for asymmetric price responses in the Alaska fixed gear ex-vessel market and price transmission from the Tokyo central wholesale market over a time period longer than a single month (here, six months). In this case, this modeling procedure is somewhat ad hoc in the sense that long-run market integration is not a maintained hypothesis, but nonetheless, the results provide good insight into the nature of short-run market integration.

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[6] The results of direct Granger causality tests discussed in footnote 3 further indicated no long-run net price leadership between the Tokyo wholesale and Pacific coast ex-vessel fixed gear markets, thereby reinforcing the conclusion of no market integration by price. Nonetheless, this relationship could have changed over 1987–89.

After experimentation with first-, second-, and third-order polynomials with a six period lag length, we estimated Equation (10) with a second-order polynomial like that given in Equation (12).[7] Direct tests of asymmetric price responses are provided by F-tests on the polynomical lag coefficients (the d's of Equation (12)) corresponding to $(b_j'' - b_j')$ in Equation (10). The parameter estimates of Equation (10) with the second-order polynomial lag are reported in Table 3 and the F-test results are reported in Table 4. A Scheffe interval[8] is used to give a more cautious test by providing a larger critical value than that given by an F-test table due to the experimentation and pretesting used to determine the degree of polynomial.

The significance test results (at a 5% level of significance with a Scheffe interval) indicate symmetric price responses, that is, the response in the Alaska fixed gear ex-vessel market to rising Tokyo wholesale market prices does not differ from responses to declining prices. The results are robust to changes in the order of polynomial from first to second to third and to inclusion or exclusion of an intercept term in Equation (10). Because a first-order polynomial did not give sensible results, the peak Alaska response to a Tokyo price change is not immediate, and does not continuously decline throughout the price transmission period.

TABLE 3.—Parameter estimates of asymmetric price linkages model. Standard errors in parentheses.

Variable	Parameter estimate
c_0	0.05761 (0.18720)
c_1	−0.01289 (0.16581)
c_2	−0.00136 (0.02676)
d_0	−0.00027* (0.00012)
d_1	0.00019 (0.00012)
d_2	−0.00003 (0.00002)

NOTE: Estimates of Equation (10) with second-order polynomial lag structure given in Equation (12). Variable abbreviations are c_i (parameters of polynomial lag for deviations from initial price) and d_i (parameters of polynomial lag for asymmetric price linkages).

* denotes statistically significant at 5%.

TABLE 4.—F-test for asymmetric price responses.

F-statistic	4.23090

F-test for overall significance of d_0, d_1, and d_2 for asymmetric price linkages.

The distributed lag estimated under the maintained hypothesis of symmetrical price responses suggests that the peak price response in the Alaska fixed gear ex-vessel market occurs by the end of the third month after a price change in the Tokyo central wholesale market. Moreover, the impact of a Tokyo central wholesale market price change dies out after the fourth month.

CONCLUDING REMARKS

In this study, we examined the Tokyo central wholesale sablefish market and the Pacific coast and Alaska ex-vessel fixed gear sablefish markets for several forms of long-run and short-run market integration and segmentation over 1981–86.

We found that the Pacific coast fixed gear ex-vessel and Tokyo central wholesale sablefish markets are segmented, so that changes in the Tokyo market prices will have no effect, immediate or lagged, on the prices of the Pacific coast market. The Pacific coast market price instead depends only upon its own lagged values and local market conditions; the ex-vessel fixed gear markets operate independently of the Tokyo central wholesale market over 1981–86. Pacific coast fixed gear harvesters of sablefish are unlikely to be adjusting their sablefish harvesting patterns in response to changes in Tokyo central wholesale market price and demand conditions. While a limited quantity of Pacific coast sablefish harvested by fixed gears is exported to Japan so that these markets are integrated by commodity flow on at least a limited scale (but not by price), the low export volume suggests that the Pacific coast producers' export strategy has not aimed at capturing an important market share or establishing a dominant position in the Japanese market. Rather, relatively small-scale U.S. producers are more likely to be simply concentrating on maximizing their net returns in any given time period. Moreover, policy actions and shifting market conditions in one country are unlikely to affect the other.

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[7] A second-order polynomial gave the most sensible shape to the actual distributed lag recovered from the polynomial lag. Moreover, we followed a nested testing procedure for determining the polynomial degree for a given lag length J suggested by Judge et al. (1980). While these results marginally suggested a third-order polynomial, the actual distributed lag (the b's in Equation (10)) recovered from the polynomial lag (given by Equation (12)) indicated a more plausible shape for the second-order polynomial. In any case, the degree of polynomial did not affect the hypothesis test results for asymmetric pricing. Beginning and endpoint constraints were not used, and to be consistent with the Ravallion approach, an intercept term was not included (which would otherwise imply an unexplained constant relationship).

[8] An F-test of linear restrictions using the Scheffe interval adjusts the confidence region, so that the F-test statistic is significant only if it exceeds in magnitude $[(a - 1) F_b]^{1/2}$, where F is the b * 100% critical value for $F(a - 1, T - a)$, T is the number of observations, and a is the number of restrictions. See Snedecor and Cochran (1976, p. 271) for details.

The Tokyo central wholesale and Alaska fixed gear ex-vessel markets are well integrated by prices in the sense of a long-run tendency in the short-run adjustment process. That is, over a period longer than one month, changes in Alaska prices can be attributed to changes in Tokyo prices and past spatial price differentials between the two markets.

Tokyo and Alaska markets are not fully integrated in the short-run, so that a price change in the Tokyo market is not fully and immediately passed on to the Alaska market within one month. Yet, a form of short-run price integration exists. Alaska market responses to rising Tokyo prices do not differ from responses to declining prices, that is, price responses are symmetric. The peak price response in the Alaska market appears to occur by the end of the third month and the impact of a Tokyo price change appears to die out after the fourth month.

Policy actions or shifting market conditions in Japan will reverberate throughout the Alaska fixed gear ex-vessel sablefish market but not in the Pacific coast fixed gear ex-vessel sablefish market. Should the Alaska fleet continue to orient its harvesting activities toward supplying the Japanese export market, it must contend with the consequent increased vulnerability to any trade, import, and fishing policies implemented by Japan as well as changes in Japanese consumer tastes and preferences. For example, Japanese policy makers might feel that sablefish imports threaten the well-being of Japanese producers domestically culturing or harvesting fish. In this case, because Alaska ex-vessel markets respond to Japanese price changes, a tariff on imported sablefish from Alaska would reduce the price received by the Alaska producers within four months. In turn, changes in Alaska's harvesting patterns would follow sometime thereafter. Alternatively, a Japanese import quota on sablefish would directly restrict the commodity flow from Alaska but not indirectly as with a tariff, which signals through the price mechanism. In contrast, because Pacific coast harvesters do not respond to the information conveyed by Tokyo prices, a Japanese import tariff would be ineffective because it would not impact any commodity flow. Thus, import quotas would be the most effective Japanese policy option to insure that commodity flows are restricted.

U.S. Alaska sablefish policies should be formulated with an eye on the market integration of the fixed gear fleet with the Tokyo market. U.S. policy intentions could be either amplified or dampened, depending upon the situation, creating unintended and perhaps even surprising consequences. For example, U.S. concern over depleting the Alaska's sablefish resource could lead to trip quotas and even contentious gear allocation issues. Yet, if Tokyo prices dramatically rise because of a subsequent restricted Alaska export flow, Alaska harvesters will receive strong market signals to increase sablefish harvests, thereby generating further pressure on the sablefish resource and aggrevating the issues of discards and gear conflicts.[9] Alternatively, if U.S. limitations on sablefish harvests are coupled with say a shift in Japanese consumers' tastes and preferences away from sablefish, leading to a pronounced decline in relative sablefish prices, Alaska producers might respond to these price signals by cutting sablefish production back below the harvest guidelines—thereby obviating the very need of these restrictions. In contrast, if the price linkages present from 1981 to 1986 continue, U.S. Pacific coast sablefish regulations can be formulated without regard to the possible effects upon U.S. production of trends and shifts in the Japanese market or Japanese government policies.

Finally, another form of vulnerability facing U.S. harvesters involves a trade parameter under less direct policy control: changes in the currency exchange rate between Japan and the United States. All prices used in this analysis are converted to U.S. dollars so that fluctuations in the exchange rate will tend to move prices of a traded good in opposite directions within the producing and consuming countries. Price movements observed in the United States and Japan from 1985 to 1987 illustrate the effect of a rapid 40% reduction in the exchange rate. As one indication of increased Japanese purchasing power, real Tokyo wholesale prices for sablefish fell by 30% during this period. At the same time, real ex-vessel prices for Alaska's longline and pot catch (nearly all of which is exported) rose by 15%, placing them at record highs. Thus the falling exchange rate sent favorable price messages to both U.S. fishers and Japanese consumers, i.e., suppliers were encouraged to provide more fish for export, while Japanese wholesalers were encouraged to buy greater quantities. It is prudent to realize, however, that a reversal in the recent exchange rate decline would tend to produce the opposite effect, sending unfavorable signals to both groups. In such a case, the rising price of the dollar would tend to lower Japanese offers for U.S. sablefish, and, in turn, lower the willingness of American producers to export, if not harvest. The more expensive dollar and reduced supplies would mean higher Japanese domestic sablefish prices, which would reduce their demand for sablefish imports.

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[9] The price of Pacific coast sablefish are also likely to bid up under this scenario. Through provision of price incentives, the Japanese will encourage methods of harvest, dress, and storage which provide a product suited to their markets (as long as the Japanese hold such a commanding price position in the market).

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8973

Development and Distribution of Larvae and Pelagic Juveniles of Three Kyphosid Fishes (*Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea*) off California and Baja California

Elizabeth G. Stevens, William Watson, and H. Geoffrey Moser

ABSTRACT: Complete developmental series are described for larvae and pelagic juveniles of three kyphosid fishes, *Girella nigricans* (Ayres), *Medialuna californiensis* (Steindachner), and *Hermosilla azurea* (Jenkins and Evermann), from California and Baja California coastal waters. Larvae of the three species have a similar compact body form, with *G. nigricans* being the most slender and *H. azurea* the most robust. They share a number of pigment characters: including dorsal, ventral, and lateral midline melanophore series; an embedded melanistic band through the eye region; and minute melanophores at the tip of the notochord. Unique pigment variations permit the identification of all developmental stages of these species. Each has a specialized pelagic juvenile stage with distinct pigmentation. The pelagic distribution of each species is described; larvae of *M. californiensis* are the most oceanic and those of *H. azurea* the most coastal of the three species. The ontogenetic characters of these species are consistent with the view that they are monophyletic.

The opaleye, *Girella nigricans*, occurs from San Francisco, California, to Cabo San Lucas, Baja California. It is a prominent member of nearshore rocky reef and kelp communities from southern California to central Baja California and ranges from the intertidal zone to about 30 m depth. The halfmoon, *Medialuna californiensis*, occurs from Vancouver Island, Canada, to the Gulf of California, but is rare north of Point Conception, California. Its preferred habitat is similar to that of *G. nigricans*, although it ranges deeper to 40 m. The zebra perch, *Hermosilla azurea*, is known from Monterey Bay, California, to the Gulf of California but prefers warmer waters and is rare north of southern California. It is found in shallow inshore areas to a maximum depth of 8 m (Miller and Lea 1972; Feder et al. 1974; Eschmeyer et al. 1983).

Opaleye and halfmoon are part of the incidental catch of the coastal purse seine fleet and are sold as "perch" in the fresh fish market (Fitch and Lavenberg 1971). Annual landings of opaleye average about 2½ tons with a maximum of 12 tons in 1973; halfmoon landings average about 7 tons annually with a maximum of 25 tons in 1968 (Heimann and Carlisle 1970; McAllister 1975). Halfmoon are seasonally abundant in the southern California commercial passenger fishing boat catch, ranking as high as fifth in numbers caught (Crook 1978). They also consistently rank among the top 10 species caught by the southern California private sport fishery (Wine 1982). Fewer opaleye are landed in these fisheries, reflecting the shallower distribution of this species; however, opaleye are a mainstay for rocky-shore anglers in southern California and are the second most important species in competitive spearfishing events (Pinkas et al. 1968; Fitch and Lavenberg 1971). Zebra perch are taken occasionally by southern California shore anglers and spearfishers (Limbaugh 1955; Feder et al. 1974).

Knowledge of the early life histories of opaleye and halfmoon is scanty. They spawn during spring and summer and their larvae appear in nearshore plankton tows during this period. Both species have a silvery pelagic juvenile stage, and both appear in small schools in nearshore areas and around floating masses of kelp. Halfmoon continue their juvenile development in these habitats, whereas opaleye enter tidepools at about 25 mm length and change abruptly to olive colored individuals which have one or two white spots on the back, lateral to the dorsal fin. They remain in the intertidal region until about

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75 mm length when they begin to seek deeper subtidal habitats (Limbaugh 1955; Fitch and Lavenberg 1971; Kramer and Smith 1973; Feder et al. 1974; Gruber et al. 1982; Walker et al. 1987; Waples 1987; Waples and Rosenblatt 1987). Information on zebra perch is limited; their larvae occur in nearshore plankton tows in summer and fall (Walker et al. 1987) and small juveniles are reported to school with those of opaleye in August (Lockley 1952; Limbaugh 1955; Feder et al. 1974).

The systematic placement of these species is unsettled. Hubbs et al. (1979) and earlier workers recognized separate families for each of them, placing *G. nigricans* in Girellidae, *M. californiensis* in Scorpididae, and *H. azurea* in Kyphosidae; other workers have grouped the three species in Kyphosidae (Robins et al. 1980). Johnson (1984) maintained separate families for these species in his survey of percoid ontogeny and included two of our original drawings (10.9 mm *G. nigricans* and 10.1 mm *M. californiensis*) in his review.

The purpose of this paper is to describe the larvae and pelagic juveniles of *G. nigricans*, *M. californiensis*, and *H. azurea*, summarize their distributions from California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys and other sources, and point out ontogenetic characters that may be useful in defining systematic relationships.

MATERIALS AND METHODS

Larvae and pelagic juveniles of *G. nigricans* and *M. californiensis* were obtained principally from CalCOFI plankton surveys, while those of *H. azurea* came from nearshore plankton samples off the San Onofre Nuclear Generating Station (SONGS) (Barnett et al. 1984). Totals of 213 larvae and 111 pelagic juveniles were available for *G. nigricans*; 253 larvae and 31 pelagic juveniles for *M. californiensis*; and 79 larvae and 6 pelagic juveniles for *H. azurea*. Additional larval specimens of *G. nigricans* were obtained from a batch of field-caught eggs reared by David Kramer in the experimental aquarium of the Southwest Fisheries Center from 1 to 28 June 1968. We reared several batches of *G. nigricans* larvae from field collections of eggs in May to July 1978 and in July 1979. None of these larvae survived more than one week; however, they were useful in defining early pigment patterns.

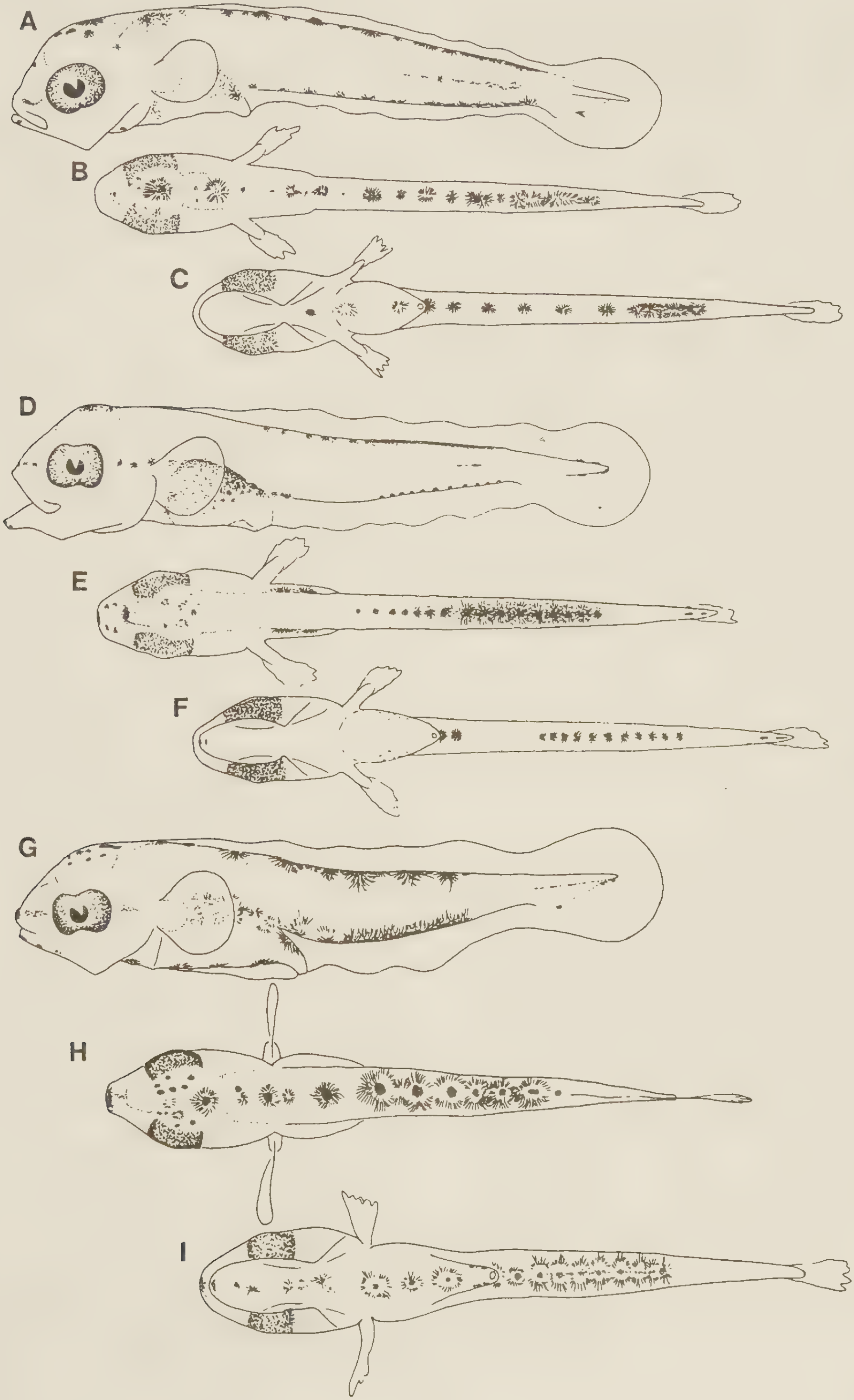
Developmental series were established to study general morphology, morphometry, and pigmentation; selected specimens were cleared and stained using the method of Potthoff (1984) to determine the sequence of ossification of fin rays, vertebrae, branchiostegal rays, and head spines. The descriptive methods and terminology follow Ahlstrom et al. (1976) and Johnson (1984). Prior to the completion of notochord flexion, body length was measured from the tip of the snout to the tip of the notochord and is designated notochord length (NL). In postflexion specimens body length was measured to the posterior edge of the hypural plate and is termed standard length (SL).

DISTINGUISHING FEATURES OF THE SPECIES

Larvae of the three species can be separated by melanistic pigment pattern (Fig. 1). Preflexion and flexion stage larvae of *G. nigricans* have one or two melanophores on the ventral midline of the gut. *Hermosilla azurea* usually have 3 or 4 (range, 1–6) evenly spaced melanophores in this region and *M. californiensis* larvae lack ventral gut melanophores during these stages. Preflexion and flexion larvae of *G. nigricans* and *H. azurea* have a series of evenly spaced melanophores along the ventral margin of the tail usually beginning at the first postanal myomere; in *M. californiensis* the series often is incomplete anteriorly (except in yolk-sac larvae). Larvae of *M. californiensis* usually have small melanophores dorsally and ventrally near the tip of the notochord. These melanophores are smaller, fewer, and often present only on the ventral margin in the other two species.

All three species are heavily pigmented along the dorsal and ventral margins through most of larval life and all three acquire a midlateral streak along the tail during notochord flexion. The streak originates more posteriorly in *M. californiensis* than in the other two species. In flexion larvae of *M. californiensis* and *H. azurea*, pigment spreads from the dorsal, lateral, and ventral series to form a band around the tail. This band originates more anteriorly

FIGURE 1.—Lateral, dorsal, and ventral views of early kyphosid larvae: (A–C) *Girella nigricans*, 5.7 mm NL, CalCOFI cruise 7805, station 90.28, surface tow; (D–F) *Medialuna californiensis*, 5.2 mm NL, CalCOFI cruise 6207–B, station 110.55, oblique tow; (G–I) *Hermosilla azurea*, 4.3 mm NL, MEC SONGS cruise I–80, surface tow.


A
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and is broader in the latter species, although in both species it subsequently expands anteriorly to completely cover the sides of the body. Late larvae and pelagic juveniles of all three species are heavily pigmented; *G. nigricans* maintains a strong midlateral stripe, *M. californiensis* becomes uniformly pigmented, and *H. azurea* develops a mottled or barred pattern.

The three species differ in body depth, with *G. nigricans* the most slender and *H. azurea* the most robust. Developmental events occur at a smaller size in *H. azurea* than in the other species. Notochord flexion occurs between 4.1 and 5.8 mm in *H. azurea*, and between 5.8 and 8.6 mm in *G. nigricans* and *M. californiensis*. Transformation to pelagic juveniles occurs at about 11–12 mm in *H. azurea*, ca. 17 mm in *G. nigricans* and ca. 12 mm in *M. californiensis*. Head spination is more developed in *M. californiensis* than in the other two species.

Dorsal and anal fin ray counts are distinct for all three species at about 10 mm SL. *Hermosilla azurea* has XI, 11 dorsal rays and III, 10 anal rays while these fin formulas are D: XII–XIV, 12–15, A: III, 10–13 for *G. nigricans* and D: IX–X, 22–27, A: III, 17–21 for *M. californiensis* (Miller and Lea 1972).

Girella nigricans

Figures 1–3

General Morphology

Our smallest yolk-sac larvae are ca. 3.0 mm, have unpigmented eyes, a rudimentary mouth, and a large oval yolk sac which extends from the head to ca. midintestine and contains a single posteriorly located oil globule (ca. 0.16–0.20 mm diameter). Larvae are 3.5–3.7 mm long when the yolk is completely absorbed. Preflexion larvae are moderately slender with a relatively short coiled gut which extends slightly less than 40% of body length (Tables 1, 2). A small gas bladder is positioned anteriorly above the gut. The head is relatively small, with a blunt snout, and with round to slightly elongate (horizontally) eyes (Fig. 2).

Development is gradual during flexion and postflexion with no abrupt changes in body form or proportions. Most body parts increase relative to body length throughout the larval period with snout-anus length, head length, and body depth showing the greatest changes (Table 2). A small blunt spine develops at the angle of the preopercle in late preflexion larvae, and remains inconspicuous during later larval stages. No other head spines develop in larvae; however, one or more additional minute preopercular spines may appear in early pelagic juveniles. These specimens also develop an opercular and a minute supracleithral spine.

Notochord flexion begins at ca. 5.8 mm length and is completed by ca. 8.6 mm. Transformation into the pelagic juvenile stage is indicated by the appearance of scales (first seen in a 15.7 mm specimen), completion of fin ray elements, and attainment of juvenile pigment at about 17 mm (Fig. 3).

Fin Formation and Meristics

The first rays to calcify are the central principal caudal rays beginning late in the preflexion stage at ca. 5.8 mm (Table 3). The full complement of 9+8 principal rays is present midway through flexion and the procurrent rays begin to calcify at the end of flexion. The full complement of 10–12+9–10 procurrent rays is acquired in early pelagic juveniles (Table 3).

The dorsal and anal soft rays begin to calcify during flexion. Addition is posteriad with full complements attained in early postflexion. Dorsal and anal spines appear during early postflexion and are added in an anteriad direction. Full dorsal and anal fin complements (D: XII–XIV, 12–15; A: III, 10–13) are present in postflexion larvae 10.7 mm and larger.

The pectoral fins are initially rounded with rounded bases and retain this shape throughout the larval period; they become more elongate in pelagic juveniles. Calcification of rays begins midway through flexion; the upper rays are the first to appear and addition is ventrad. The full complement of 18–20 is present just before transformation into the pelagic juvenile.

The pelvic fins are the last to form. Fin buds appear midway through flexion and calcification of rays begins just after flexion is completed. The full complement of I,5 rays was present in specimens 10.7 mm and larger.

Initial vertebral ossification was not apparent in our stained series; however, the anteriormost 22 vertebral centra were already ossifying in a 6.7 mm larva. Ossification proceeds in a posteriad direction and the full complement of 27 vertebrae is present by the end of flexion. The branchiostegal rays begin to ossify late in preflexion and the full complement of six pairs of rays is present late in flexion.

TABLE 1.—Measurements (mm) of larvae and pelagic juveniles of *Girella nigricans*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
6606–93.27	2.6	0.96	0.54	0.60	0.10	0.34	0.54	—	—	—	—
6307–83.39	2.7	0.86	0.51	0.44	0.08	0.28	0.46	0.14	—	—	—
8105–83.3.42	2.8	1.1	0.56	0.58	0.08	0.24	0.46	0.20	0.10	—	—
6606–93.27	2.9	1.2	0.65	0.74	0.09	0.22	0.60	0.20	0.10	—	—
8105–83.3.42	3.0	1.1	0.62	0.58	0.14	0.20	0.50	0.22	0.11	—	—
8105–83.3.42	3.1	1.1	0.64	0.64	0.16	0.20	0.56	0.30	—	—	—
6606–93.27	3.2	1.2	0.74	0.70	0.16	0.32	0.60	0.30	0.14	—	—
6509–120.40	3.4	1.4	0.45	0.48	0.11	0.26	0.45	—	—	—	—
6110–127.34	3.5	1.2	0.71	0.62	0.11	0.29	0.54	0.30	—	—	—
8105–83.3.42	3.6	1.2	0.72	0.66	0.12	0.26	0.60	—	—	—	—
SCBSIII 303	3.8	1.4	0.78	0.64	0.11	0.30	0.60	0.40	0.18	—	—
5710–123.37	4.1	1.8	1.0	0.80	0.22	0.34	0.79	0.60	0.22	—	—
SCBSIII 303	4.2	1.7	0.88	0.80	0.12	0.36	0.70	0.40	—	—	—
8105–103.3.29	4.3	1.8	1.0	0.80	0.22	0.42	0.78	0.46	0.18	—	—
5607–97.40	4.4	1.6	1.1	0.82	0.18	0.40	0.76	0.32	—	—	—
5708–127.34	4.5	1.8	0.86	0.84	0.23	0.33	0.80	0.44	0.16	—	—
8108–106.7.31	4.7	1.8	1.3	0.94	0.28	0.50	1.0	—	0.24	—	—
6310–87.32.5	4.8	2.0	1.2	0.96	0.24	0.42	0.84	0.60	0.22	—	—
6507–93.26	4.9	1.9	1.1	0.92	0.21	0.41	0.88	0.80	—	—	—
7805–90.28	5.8	2.0	1.4	1.1	0.32	0.52	1.0	0.60	0.36	—	—
5910–127.34	6.0	2.3	1.5	1.3	0.40	0.54	1.2	0.60	0.36	—	—
8107–83.3.42	6.1	2.3	1.5	1.2	0.36	0.56	1.3	0.60	0.34	3.2	—
8105–103.3.29	6.2	2.3	1.6	1.2	0.24	0.60	1.2	0.60	0.42	3.2	1.8
7805–90.28	6.3	2.4	1.5	1.2	0.36	0.60	1.2	0.64	0.36	3.3	—
8105–103.3.29	6.4	2.5	1.7	1.1	0.42	0.56	1.1	0.80	0.36	3.4	—
7805–90.28	6.5	2.3	1.6	1.2	0.32	0.60	1.2	0.88	0.40	3.3	1.5
8107–93.3.50	6.6	2.6	1.4	1.4	0.34	0.66	1.4	1.0	0.50	4.0	2.1
8107–93.3.50	6.7	2.7	1.8	1.5	0.46	0.72	1.5	0.80	0.30	3.7	2.1
7805–90.28	6.8	2.5	1.8	1.3	0.34	0.62	1.3	0.60	0.32	3.8	2.0
7805–90.28	7.0	2.8	1.9	1.4	0.40	0.68	1.4	0.82	0.40	4.0	2.0
7805–90.28	7.1	2.8	2.0	1.4	0.42	0.68	1.4	0.76	0.56	3.9	2.0
8105–103.3.29	8.2	3.6	2.4	1.7	0.48	0.88	1.8	1.1	0.42	3.8	2.7
8107–80.51	8.4	3.8	2.4	1.7	0.40	0.84	1.7	0.92	0.54	4.8	2.5
8105–86.7.35	8.6	3.7	2.5	1.8	0.60	0.88	1.9	1.2	0.56	4.0	2.8
8105–86.7.45	8.6	4.0	2.8	2.1	0.60	0.88	2.2	1.2	0.70	3.8	2.9
8105–86.7.33	10.7	5.5	3.1	2.2	0.64	1.1	2.5	—	0.68	3.9	3.4
7803–90.60	11.9	5.7	3.3	2.0	0.74	1.2	2.5	1.8	0.68	3.8	3.8
8108–96.7.35	14.8	8.1	4.9	3.8	1.0	1.6	3.8	2.6	0.80	5.7	5.2
8107–93.3.55	15.8	8.5	5.0	3.4	1.2	1.5	3.8	3.2	0.92	5.2	5.2
8107–93.3.55	16.5	8.3	5.2	3.7	1.2	1.6	4.1	2.8	1.0	6.0	6.0
8107–80.55	17.3	9.2	5.5	3.7	1.3	1.8	4.2	3.3	1.2	5.8	5.7
8108–103.3.30	18.4	10.3	5.8	4.5	1.5	1.8	5.0	3.4	1.2	6.8	6.7
8102–120.30	19.5	10.8	5.8	4.6	1.4	1.8	5.1	4.8	1.2	6.9	6.4
6612–123.36	23.2	12.0	6.9	5.8	1.8	2.2	6.7	5.0	1.6	8.2	7.7

TABLE 2.—Average body proportions (% ± standard deviation) for larvae of

Species/stage	Snout-anus length / Body length	Head length / Body length	Head depth / Body length	Snout length / Body length	Eye diameter / Body length
Girella nigricans					
Preflexion	38.2 ± 2.92	21.5 ± 3.07	19.3 ± 2.49	4.1 ± 1.06	8.7 ± 1.58
Flexion	38.9 ± 2.91	25.8 ± 2.15	19.8 ± 1.35	5.6 ± 0.82	9.6 ± 0.60
Postflexion	49.6 ± 4.15	30.7 ± 2.05	21.8 ± 2.88	6.8 ± 0.57	10.1 ± 0.42
Juvenile	54.1 ± 1.99	30.7 ± 1.13	23.6 ± 1.57	7.7 ± 0.43	9.7 ± 0.51
Medialuna californiensis					
Preflexion	39.6 ± 2.49	21.2 ± 3.23	19.1 ± 2.09	4.1 ± 1.23	8.4 ± 0.64
Flexion	44.3 ± 4.31	27.2 ± 3.88	21.8 ± 2.21	6.3 ± 0.86	10.7 ± 1.15
Postflexion	50.6 ± 4.13	30.5 ± 3.29	23.3 ± 1.46	6.0 ± 0.75	10.8 ± 0.33
Juvenile	56.5 ± 2.29	33.4 ± 1.75	27.2 ± 2.05	6.7 ± 0.92	10.6 ± 0.70
Hermosilla azurea					
Preflexion	51.0 ± 3.23	28.4 ± 3.10	23.5 ± 3.31	6.1 ± 1.66	11.0 ± 0.47
Flexion	54.2 ± 3.06	31.9 ± 3.90	24.0 ± 3.42	7.9 ± 1.46	11.6 ± 1.06
Postflexion	57.3 ± 1.03	31.7 ± 2.25	25.8 ± 1.72	7.5 ± 0.55	12.2 ± 0.75
Juvenile	58.0 ± 1.83	32.8 ± 1.89	25.8 ± 2.06	6.5 ± 0.58	11.2 ± 0.96

Pigmentation

Pigmentation of yolk sac and early preflexion larvae was described by Orton (1953) from specimens cultured in the laboratory. Newly hatched larvae have a few melanophores on the hindgut and in a short midventral row at the base of the tail. At about midway through yolk absorption, small melanophores appear on the ventral surface of the yolk sac (Fig. 2A); the row above the hindgut becomes heavier, extending forward to about the midpoint of the yolk sac; and the midventral tail series has increased to 7–11 melanophores, extending posteriad along most of the tail. A series of small melanophores appears on the dorsal midline along the posterior half of the tail, and several small melanophores are present above and below the tip of the notochord. Near the end of yolk absorption the eyes become pigmented; the dorsal gut pigment becomes heavier and extends over the entire gut; and the ventral tail melanophores enlarge, partly by aggregation, as do the melanophores on the dorsal margin of the tail.

In early preflexion larvae the ventral midline series of 5–8 large melanophores is continuous with the dorsal gut melanophores. A space separates the ventral tail series from one or more smaller melanophores near the tip of the notochord. The dorsal midline series consists of ca. 1–4 large melanophores posteriorly on the tail, with one to several small melanophores near the tip of the notochord. A large melanophore develops above the midbrain and one forms on the nape. Internal pigment develops below each otic capsule, appearing as a continuation of the dorsal gut pigment. The series of small ventral gut melanophores coalesces into 3 pigment loci, each usually containing a single melanophore: 1) an embedded melanophore anterior to the liver, 2) a surface midventral spot just posterior to the liver, 3) a surface midventral spot just anterior to the hindgut (Fig. 1C).

During preflexion the dorsal gut pigment expands to the lateral surface of the gut. The dorsal midline series increases anteriorly beginning in early preflexion, and soon extends from the head nearly to the tip of the tail. The smaller melanophores near the tip of the tail disappear or are reduced to one. Dorsal melanophores number 11–15. The smaller ventral spots at the notochord tip disappear, except for one, which persists in the finfold about halfway between the end of the ventral pigment series and the tip of the tail.

During late preflexion and flexion stages, pigment increases on the midbrain and appears on both the forebrain and hindbrain. Paired melanophores develop on the roof of the mouth below the nasal capsules and olfactory lobes, and one or more form at the tip of the lower jaw. As the pigment associated with the otic capsule increases, an embedded stripe passing through the eye region is formed (Fig. 2E). One or two surface melanophores appear posterior to the eye in the opercular region. Melanophores appear on the tip of the lower jaw, at the angle of the jaw, and later along the rami of the jaw. A large

Girella nigricans, *Medialuna californiensis*, and *Hermosille azurea*.

Species/stage	Body depth / Body length	Pectoral fin length / Body length	Pectoral fin base depth / Body length	Predorsal length / Body length	Prepelvic length / Body length
Girella nigricans					
Preflexion	17.6 ± 1.98	9.7 ± 3.00	4.3 ± 0.69		
Flexion	19.8 ± 1.58	11.3 ± 1.79	6.0 ± 0.97	54.0 ± 3.69	29.4 ± 2.83
Postflexion	23.8 ± 1.77	16.3 ± 2.42	6.3 ± 0.89	37.7 ± 4.81	33.4 ± 1.68
Juvenile	26.6 ± 1.92	21.0 ± 2.78	6.6 ± 0.34	35.3 ± 1.43	33.8 ± 1.72
Medialuna californiensis					
Preflexion	17.0 ± 2.22	10.2 ± 1.29	4.7 ± 1.44		
Flexion	22.4 ± 2.49	12.2 ± 2.05	6.8 ± 0.83	44.8 ± 6.69	34.5 ± 2.43
Postflexion	24.2 ± 2.23	16.8 ± 3.46	6.6 ± 0.72	42.4 ± 5.80	33.8 ± 2.62
Juvenile	29.3 ± 0.71	22.0 ± 1.53	6.2 ± 0.74	38.1 ± 2.12	38.1 ± 1.13
Hermosilla azurea					
Preflexion	22.5 ± 2.59	12.0 ± 0.82	7.9 ± 1.12		
Flexion	24.5 ± 2.33	12.9 ± 2.23	9.1 ± 0.83	39.4 ± 1.99	36.6 ± 0.40
Postflexion	25.8 ± 1.17	16.4 ± 4.16	7.8 ± 0.98	40.3 ± 2.42	39.3 ± 2.42
Juvenile	31.2 ± 1.50	25.0 ± 2.45	7.2 ± 0.50	40.2 ± 1.26	38.5 ± 1.91

TABLE 3.—Meristics of cleared and stained specimens of *Girella nigricans*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin rays	Anal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
5.8	3	3	—	—	3	3	—	—	—	—	—	—	—
6.0	6	6	—	—	4	4	—	—	—	—	—	—	—
6.5	8	7	—	—	5	5	—	—	—	—	—	—	—
6.7	8	7	—	—	5	5	—	—	—	—	—	—	22
7.0	9	8	—	—	5	5	—	—	—	—	—	—	24
7.2	9	8	—	—	6	6	6	6	5	—	—	—	26
7.9	9	8	1	1	6	6	10	10	13	10	—	—	27
8.2	9	8	1	1	6	6	9	10	12	10	1	1	27
9.1	9	8	1	1	6	6	14	14	—	—	I,4	I,4	27
10.7	9	8	5	5	6	6	17	17	XIII,14	III,12	I,5	I,5	27
11.7	9	8	6	5	7	7	17	17	XIII,15	III,11	I,5	I,5	27
12.0	9	8	5	5	6	6	18	18	XIII,13	III,11	I,5	I,5	27
15.7	9	8	10	9	6	6	20	20	XIII,12	III,11	I,5	I,5	27
21.8	9	8	12	9	6	6	19	19	XIV,13	III,11	I,5	I,5	27
22.0	9	8	10	10	6	6	18	19	XV,13	III,11	I,5	I,5	27
37.0	9	8	11	10	6	6	19	19	XIV,13	III,10	I,5	I,5	27

melanophore appears on the isthmus just anterior to the gut, often preceded by a series of several smaller spots. The pigment on the ventral surface of the gut may also increase to form a series of pigment dashes.

At this stage a line of midlateral pigment dashes develops on the tail, posteriorly between the dorsal and ventral midline pigment. The lateral row expands anteriad, reaching the trunk by the end of flexion. Pigment becomes heaviest posteriorly, and when midlateral, midventral, and middorsal melanophores are expanded in this region, an incomplete bar is formed. Concurrent with the development of the lateral midline pigment, internal series of melanophores form above and below the vertebral column and expand anteriorly in concert with the external lateral series.

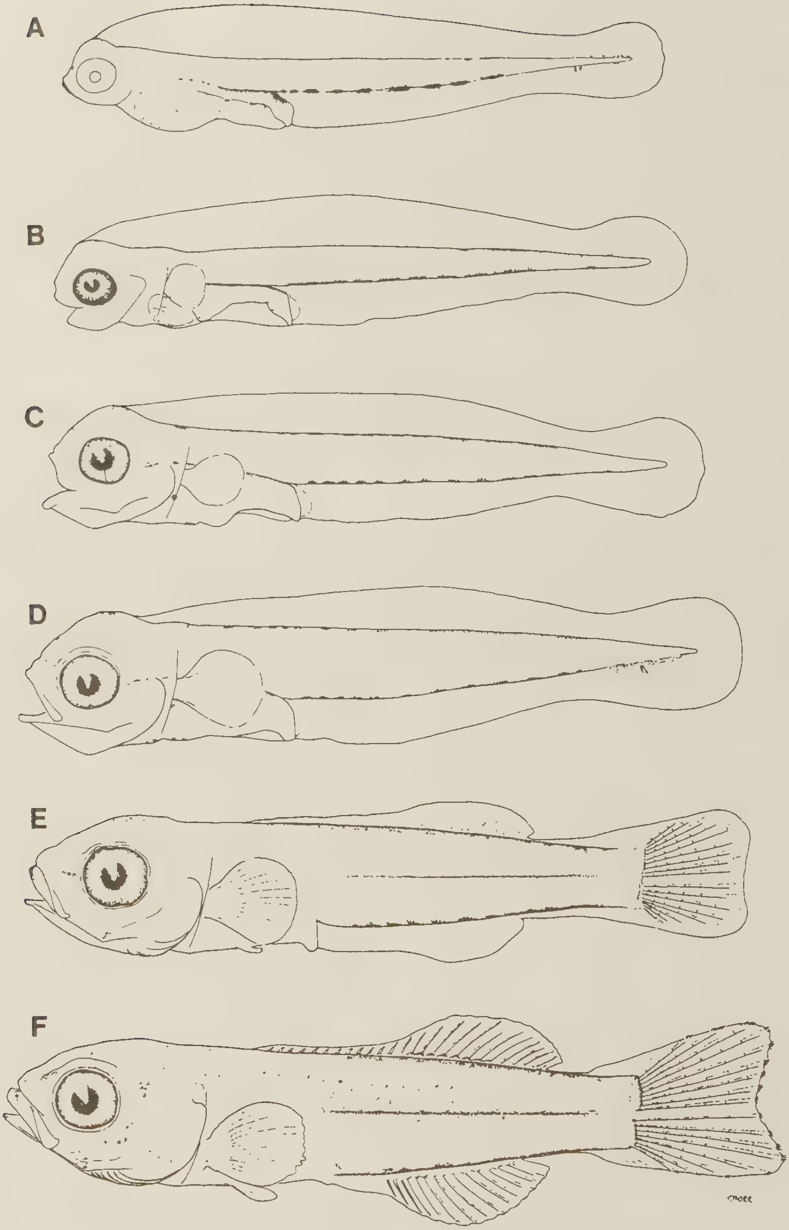

FIGURE 2.—Reared larvae of *Girella nigricans*: (A) 3.8 mm NL, day 1; (B) 3.8 mm NL, day 2; (C) 4.6 mm NL, day 8; (D) 5.3 mm NL, day 10; (E) 7.8 mm SL, day 18; (F) 10.9 mm SL, day 22.

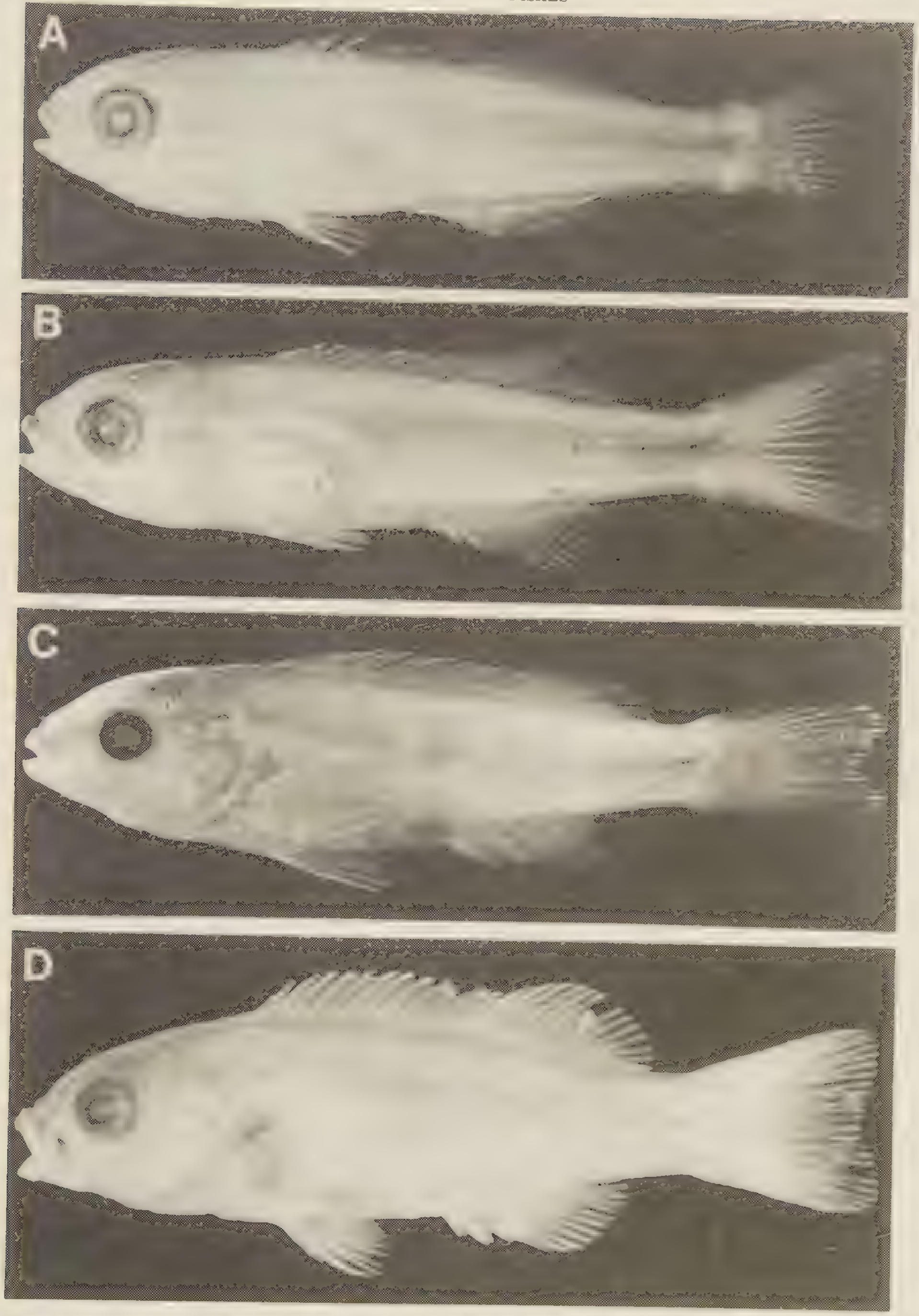

FIGURE 3.—Pelagic juveniles of *Girella nigricans*. (A) 15.8 mm SL, CalCOFI cruise 8107–JD, station 93.3.55, surface tow; (B) 17.3 mm SL, CalCOFI cruise 8107–JD, station 80.55, surface tow; (C) 22.8 mm SL, SIO Marine Vertebrate Collection, Cat. No. 76–295; (D) 29.0 mm SL, MEC SONGS cruise I–28, surface tow.

The caudal melanophore (Fig. 2D) becomes located at the posterior hypural margin between the superior and inferior elements, and remains prominent during flexion. By the end of flexion it is accompanied by 1–5 more melanophores which outline the posterior edge of the hypural plate.

By the end of flexion the sides of the gut are covered with melanophores, the dorsal midline pigment is continuous to the head, and the lateral midline series extends slightly forward of the vent. A line of pigment extends along the isthmus; pigment outlines the jaw on its ventral surface; and pigment increasingly covers the snout, dorsal surface of the head, opercles, pectoral fin bases, and the walls of the gill chambers.

During postflexion and early juvenile stages the amount of head and body pigment continues to increase. The lateral body stripe enlarges dorsad, ventrad, and anteriad. Small melanophores begin to outline the myosepta, initially in the epaxial zone and later in the hypaxial zone. Eventually the areas between the myosepta fill with melanophores and the entire body and head are covered (Fig. 3D). In addition to the development of melanistic pigment, early juveniles develop a layer of guanine which produces a silvery sheen on the lower half of the body. This silvery condition is retained throughout the pelagic phase and is lost abruptly when the pelagic young enter the tidepools at 25 mm length (Feder et al. 1974).

Fin pigment appears in early juveniles when the dorsal spines become outlined with mela-

TABLE 4.—Measurements (mm) of larvae and pelagic juveniles of *Medialuna californiensis*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
5407–97.30	2.6	0.90	0.39	0.48	0.08	0.20	0.38	—	—	—	—
6607–87.55	2.8	1.2	0.60	0.58	0.08	0.22	0.44	0.30	0.14	—	—
7805–70.90	3.1	1.2	0.66	0.56	0.10	0.26	0.54	0.28	0.10	—	—
6606–90.60	3.3	1.2	0.50	0.50	0.08	0.23	0.44	0.24	0.10	—	—
6606–87.33	3.5	1.4	0.68	0.54	0.10	0.28	0.48	0.38	0.14	—	—
6907–93.30	3.8	1.6	0.84	0.74	0.22	0.32	0.68	0.44	0.18	—	—
6907–93.30	4.0	1.7	1.0	0.76	0.22	0.34	0.72	0.40	0.18	—	—
5104–107.70	4.3	1.7	0.98	0.90	0.19	0.38	0.80	0.42	0.14	—	—
6107–83.65	4.6	1.9	1.1	0.90	0.18	0.40	0.88	0.45	0.32	—	—
6207–100.45	5.0	1.9	1.2	0.96	0.24	0.44	0.84	0.60	0.20	—	—
6207–100.35	5.2	2.0	1.2	1.1	0.26	0.48	1.0	0.50	0.28	—	—
8105–100.70	5.5	2.2	1.2	1.2	0.32	0.50	1.1	0.60	0.40	—	—
5507–103.70	5.8	2.4	1.4	1.2	0.35	0.66	1.2	0.60	0.40	2.1	—
8105–100.35	6.0	2.4	1.2	1.2	0.32	0.58	1.2	0.60	0.35	—	—
6507–100.40	6.5	2.5	1.8	1.2	0.44	0.60	1.2	0.88	0.40	3.4	—
8105–100.70	6.7	2.9	1.7	1.7	0.40	0.80	1.6	0.76	0.56	3.5	—
8107–86.7.50	7.2	3.4	2.3	1.6	0.44	0.88	1.8	0.88	0.52	3.5	2.6
8108–100.40	7.9	4.0	2.4	1.8	0.64	0.88	2.0	1.3	0.48	2.9	2.8
7808–67.65	8.1	3.6	2.3	1.7	0.54	0.76	1.8	1.0	0.52	3.6	2.5
5907–103.50	8.4	4.1	2.5	2.0	0.48	0.88	2.0	1.0	0.60	3.6	3.0
7808–67.65	9.0	4.2	2.6	2.0	0.56	0.96	2.0	1.2	0.64	4.7	3.0
7808–67.65	9.2	4.1	2.4	2.0	0.42	0.96	2.0	1.3	0.64	4.1	2.9
7808–67.65	9.5	4.9	3.3	2.3	0.60	1.0	2.3	1.4	0.72	4.0	3.1
7808–93.45	9.8	5.2	3.2	2.4	0.64	1.1	2.5	1.9	0.64	4.1	3.1
5208–90.45	10.0	5.2	2.8	2.2	0.60	1.1	2.4	1.7	0.60	3.5	3.6
7808–93.45	10.8	6.0	3.5	2.7	0.72	1.2	3.0	2.4	0.62	4.2	4.1
5208–110.60	11.8	6.8	3.8	3.2	0.72	1.3	3.5	2.4	0.76	4.6	4.3
5208–110.60	12.9	7.3	4.2	3.1	0.72	1.3	3.6	2.8	0.84	5.0	5.1
7808–100.45	13.2	7.8	4.6	3.8	1.0	1.4	4.0	2.9	0.88	5.2	5.3
5208–90.45	13.5	7.8	4.7	3.8	0.96	1.5	4.0	3.3	0.96	5.3	5.2
7210–90.70	13.7	7.8	4.9	4.0	1.1	1.6	4.1	3.0	0.84	5.4	5.2
5208–90.45	17.9	9.7	5.6	4.8	1.1	1.9	5.3	4.3	0.96	6.5	6.7
7210–90.70	21.5	11.3	7.1	5.5	1.3	2.0	6.2	4.5	1.1	7.3	8.1

nophores. Gradually the fin membrane becomes covered with melanophores as does the basal half of the soft dorsal fin. Anal fin pigment is limited to a few anterior melanophores, and the caudal and the paired fins remain unpigmented.

Medialuna californiensis

Figures 1, 4, 5

General Morphology

The smallest yolk-sac larva in our collection is 2.6 mm long; it has a large oval yolk sac, a single posteriorly located oil globule (0.20 mm diameter), unpigmented eyes, and lacks a mouth (Fig. 4A). Larvae are ca. 3.0 mm long at the completion of yolk absorption; development is gradual with no abrupt changes in body form (Tables 2, 4).

The first head spines appear during flexion on the posterior preopercular margin near the angle. A 6.1 mm larva has 2 spines. The number of spines increases up to 6 in preflexion larvae and to 10–13 spines in juveniles up to 21.5 mm. In larger juveniles the spines are blunt and the posterior preopercular margin is smooth in a 33.7 mm juvenile. A single spine is present on the anterior preopercular ridge in a 6.5 mm larva. This spine is variously present or absent in flexion and postflexion larvae, and is absent in juveniles larger than 13.8 mm in our collections. A single spine is present at the edge of the subopercle in larvae as small as 7.1 mm and is found on all postflexion larvae and juveniles up to a length of 21.5 mm. An interopercular spine is present in all postflexion larvae and in juveniles up to 18.2 mm. A supracleithral spine appears late in the postflexion stage (at 10.1 mm) and a posttemporal spine appears at 12.8 mm. Both spines are present in juveniles up to 21.5 mm but are absent in larger specimens. An opercular spine is present in juveniles between 12.8 and 21.5 mm. A cleithral spine is present on a single 18.2 mm juvenile.

Notochord flexion begins at ca. 5.8 mm and is completed at ca. 8.6 mm (Table 5). Transformation into the pelagic juvenile occurs at ca. 12 mm (Fig. 5).

Fin Formation and Meristics

The first rays to form are the principal caudal rays early in flexion (Table 5). The full complement of 9+8 rays is present at midflexion, when the procurrent rays begin to develop. The full complement of 11–13 + 10–11 procurrent rays is present in early juveniles.

Dorsal, anal, and pectoral rays begin to calcify during midflexion in the manner described for *G. nigricans*. Full complements of dorsal (IX–X, 22–27) and anal (III, 17–21) rays form in early postflexion larvae (Table 5). The full complement

TABLE 5.—Meristics of cleared and stained specimens of *Medialuna californiensis*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin rays	Anal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
6.1	6	5	—	—	4	4	—	—	—	—	—	—	12
6.5	9	8	—	—	6	6	—	—	—	—	—	—	21
7.1	9	8	1	1	7	7	10	10	20	II,16	—	—	24
7.4	9	8	1	1	7	6	8	8	19	14	—	—	24
8.1	9	8	—	1	6	6	6	6	9	9	—	—	24
8.6	9	8	2	2	7	7	10	10	VI,22	II,18	—	—	25
9.1	9	8	3	3	7	7	14	14	IX,22	III,18	—	—	25
9.5	9	8	4	4	7	7	14	14	VIII,22	III,17	I,2	I,2	25
10.1	9	8	5	5	7	7	14	14	X,24	III,19	I,4	I,4	25
11.0	9	8	6	6	7	7	17	17	X,23	III,18	I,5	I,5	25
12.8	9	8	9	8	7	7	18	18	X,24	III,19	I,5	I,5	25
13.8	9	8	11	10	7	7	17	17	X,25	III,19	I,5	I,5	25
18.2	9	8	13	11	7	7	18	18	X,25	III,19	I,5	I,5	25
21.5	9	8	12	11	7	7	18	18	X,25	III,19	I,5	I,5	25
27.6	9	8	12	11	7	7	18	17	X,23	III,18	I,5	I,5	25
33.7	9	8	12	11	7	7	19	20	X,23	III,18	I,5	I,5	25

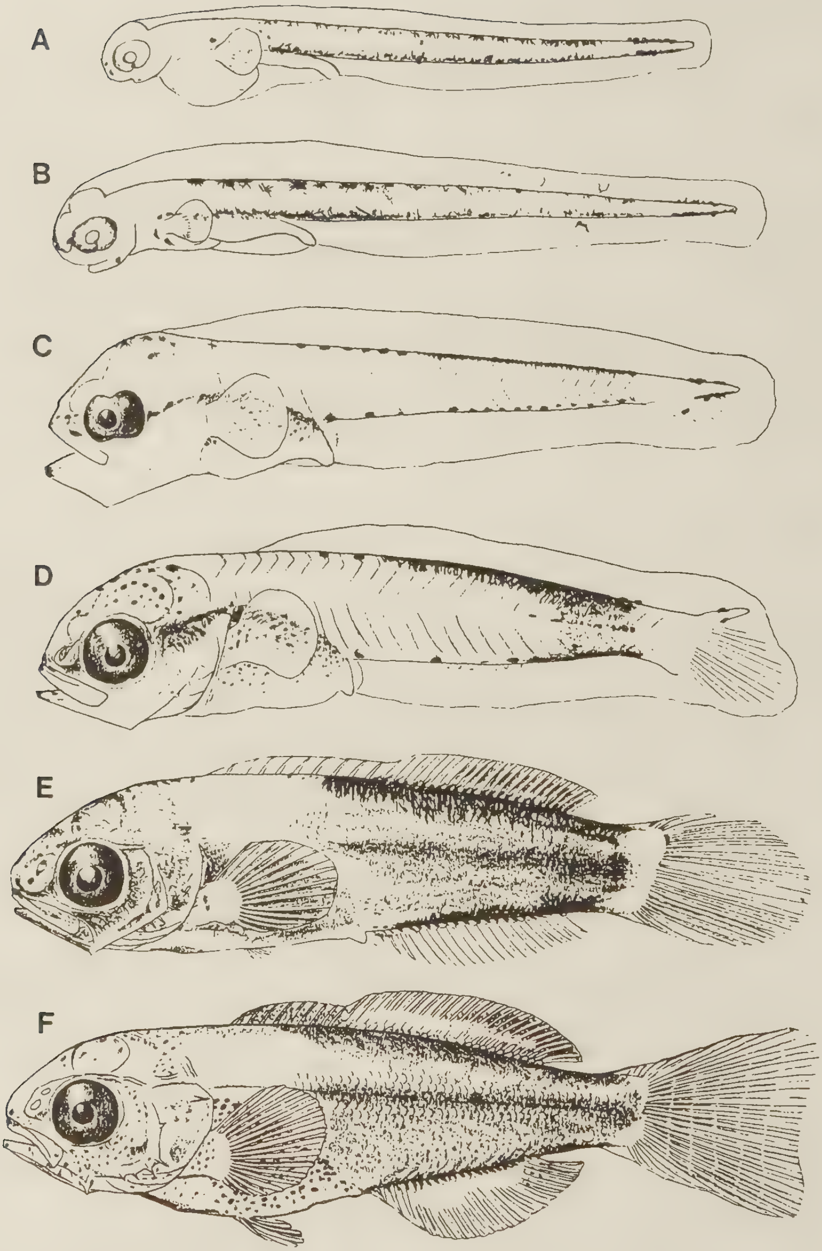

FIGURE 4.—Larvae of *Medialuna californiensis* from CalCOFI oblique plankton tows: (A) 3.0 mm NL, cruise 5004, station 120.90; (B) 3.5 mm NL, same station as above; (C) 4.7 mm NL, cruise 4906, station 102.75; (D) 6.8 mm NL, cruise 4907, station 92.68; (E) 10.1 mm SL, cruise 5007, station 100.70; (F) 11.8 mm SL, cruise 4910, station 82.77.

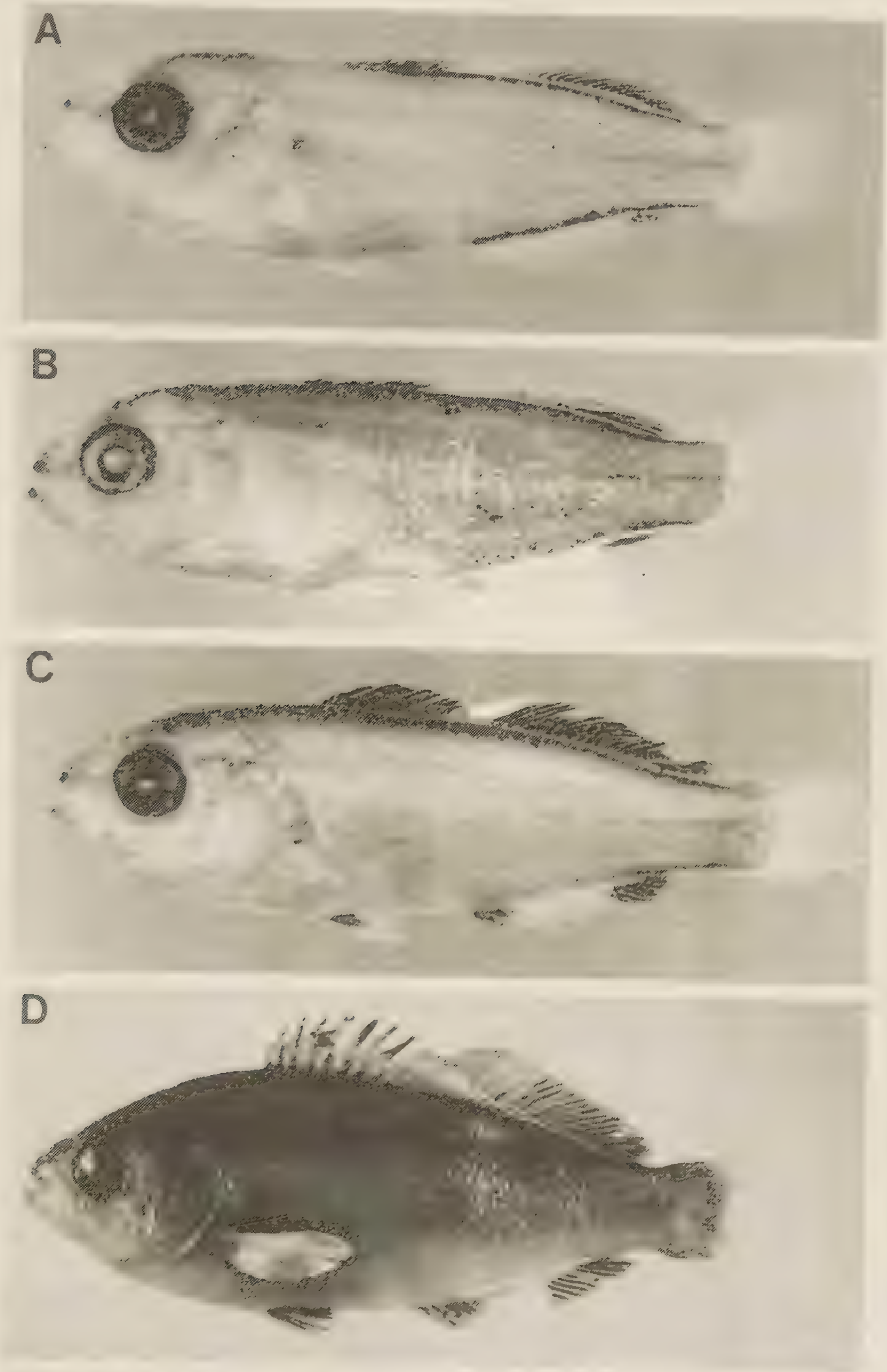

FIGURE 5.—Pelagic juveniles of *Medialuna californiensis*: (A) 13.2 mm SL, CalCOFI cruise 7808, station 100.45, surface tow; (B) 17.9 mm SL, CalCOFI cruise 5208, station 90.45, surface dipnet; (C) 20.5 mm SL, CalCOFI cruise 5407-H, station 130.60, surface dipnet; (D) 46.0 mm SL, SWFC DSJ midwater trawl, off Catalina Island, 31 October 1968.

of 17–20 pectoral rays appears at transformation. Pelvic rays begin to calcify late in postflexion and all are calcifying at transformation. Initial vertebral ossification occurs early in the flexion stage and the full complement of 25 vertebrae is present at the end of flexion. Calcification of branchiostegal rays begins late in preflexion and the full complement of 7 pairs is present in some midflexion specimens.

Pigmentation

The earliest yolk-sac larvae in our collections have extensive dorsal and ventral midline pigment. The dorsal midline has an irregular row of 30–40 melanophores between the notochord tip and the midgut region. More than 40 melanophores form an irregular series along the entire ventral margin of the tail, extending some distance forward above the gut. Melanophores in these rows coalesce to ca. 30 in each, before the eyes become pigmented. At initial eye pigmentation there are ca. 20 larger, regularly arranged melanophores in each row with a gap separating a line of 5–7 smaller melanophores that outline the dorsal and ventral margins of the notochord tip. Melanophores also appear at the dorsal surface of the gut, at the gular region, and on the snout.

At the end of the yolk-sac stage the melanophores in the dorsal and ventral rows coalesce to as few as 18 in the dorsal row and to 16 in the ventral row. A melanophore forms at the nape and, in some specimens, is continuous with the dorsal midline series. The zone of melanophores covering the dorsal surface of the gut extends forward into the head below the otic region. Embedded melanophores form in the snout region below the forebrain and some appear above the midbrain. The ventral gut melanophores move internally anterior to the gut mass. A melanophore is present at the tip of the lower jaw.

The midline melanophores coalesce further during early preflexion (15–18 dorsally and 12–15 ventrally). The short rows at the notochord tip are also reduced (2–3 dorsally and 1–3 ventrally). Melanophores are added above the brain and cover the optic lobes. Snout and otic pigment increase to give the appearance of a band through the eye, similar to that formed in *G. nigricans* and *H. azurea* (Fig. 1D, 4C). The dorsal gut melanophores increase to form a shield which extends laterally over the gut; the ventral surface of the gut remains unpigmented.

Midlateral melanophores begin to form posteriorly on the tail in preflexion larvae as small as 3.8 mm. The series consists of 1–2 (up to 4) melanophores during most of the preflexion period. During this period the dorsal midline series recedes posteriad to above the hindgut and a gap develops in the ventral series posterior to the large melanophore embedded above the anus. In late preflexion and flexion larvae the ventral series is restricted to the posterior half of the tail and contains 6–10 melanophores. Melanophores are added to the lateral series during flexion and a short bar is formed when these, together with the midline melanophores above and below, are expanded. By the end of flexion it is difficult to distinguish individual melanophores in any of the midline series. The melanistic shield on the gut covers all but the ventral midline. The dorsal surface of the head is fully pigmented and a patch of melanophores forms on the opercle. The notochord tip usually has 1–2 small melanophores dorsally and ventrally in flexion larvae, 0–2 in postflexion specimens, and 0–2 in some pelagic juveniles up to 14.5 mm in length.

The dorsal and ventral midline pigment series extend forward in postflexion larvae, the ventral series reaching the anus at ca. 9.5 mm and the dorsal series reaching the head at ca. 10.5 mm. The lateral midline series reaches the anal fin origin at ca. 9.0 mm and extends to above the midgut in transforming larvae. A covering of superficial melanophores develops on the tail and advances anteriad with the midline series. The entire body, except for the anterior trunk region, is pigmented by the end of postflexion and only a small portion of the upper trunk lacks melanophores in transforming specimens. Melanophores are added to the opercular and preopercular regions, the lower jaw, gular region, and isthmus. The entire head and gut are pigmented by the beginning of transformation.

The distinctive fin pigmentation of pelagic juveniles begins to form in late postflexion larvae when the membrane between the posterior dorsal soft rays becomes pigmented (Fig. 4E, 4F). By the end of transformation the membrane between the dorsal spines also becomes pigmented, leaving an unpigmented zone in the middle of the fin. Also, at this stage a melanistic zone develops posteriorly on the anal fin (Fig. 5A). A patch develops over the anal spines and basally on each pelvic fin in 14.0 mm pelagic juveniles; juveniles up to about 40 mm are characterized by this interrupted pattern on the median fins (Fig. 5C). In 40–50 mm juveniles the entire dorsal fin is pigmented except for an area on the anterior half of the soft dorsal. The pelvic fins are completely pigmented at 50 mm. The pectoral and caudal fins are unpigmented in larvae and pelagic juveniles.

Hermosilla azurea

Figures 1, 6, 7

General Morphology

The size and state of development at hatching are unknown. The smallest larva examined, 2.5 mm, had pigmented eyes, a functional mouth, and no remnants of yolk or oil droplets. Preflexion larvae are moderately robust, with a coiled gut extending slightly beyond midbody (Tables 2, 6) and with a small swimbladder over the anterior gut. The head is moderately large, with a blunt snout, and with round to slightly elongate (horizontally) eyes. Development is gradual with no abrupt changes in body form or proportions. Most body parts showed small increases in size relative to the standard length (Table 2). Among the largest proportional changes are the increases in snout-anus length and in body depth (Fig. 6).

Larvae acquire only a few small head spines. The first spine may develop at the angle of the posterior preopercular margin as early as late preflexion (3.7 mm), or may be delayed until early flexion (always present by 4.7 mm); 19% of preflexion larvae had this spine. During flexion 1–3 additional small spines develop along the posterior preopercular margin and up to 3 (usually 0 or 1) small spines are acquired along the anterior preopercular ridge. Postflexion larvae may develop up to 4 very small spines along the posterior margin of the subopercular, and usually lose the anterior preopercular spines. Juveniles lack both the preopercular and the subopercular spines.

TABLE 6.—Measurements (mm) of larvae and pelagic juveniles of *Hermosilla azurea*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
SONGS	2.5	1.2	0.56	0.64	0.08	0.28	0.44	0.28	0.16	—	—
	2.8	1.4	0.76	0.72	0.20	0.32	0.60	—	0.24	—	—
	3.0	1.6	0.84	0.72	0.16	0.36	0.64	0.32	0.28	—	—
	3.2	1.8	1.0	0.88	0.24	0.36	0.80	—	0.24	—	—
	3.4	1.7	0.92	0.56	0.16	0.36	0.72	0.40	0.28	—	—
	3.6	1.8	1.1	0.72	0.28	0.40	0.88	0.44	0.24	—	—
	3.8	2.1	1.2	0.96	0.32	0.44	1.0	—	0.24	—	—
	4.0	1.8	1.1	0.92	0.24	0.44	0.88	0.56	0.36	—	—
	4.4	2.1	1.1	0.92	0.28	0.44	0.92	0.52	0.36	—	—
	4.6	2.4	1.4	1.2	0.24	0.52	1.2	0.60	0.40	—	—
SONGS	4.1	2.2	1.4	1.0	0.36	0.48	1.0	0.42	0.40	—	—
	4.3	2.4	1.4	0.88	0.36	0.52	1.0	0.64	0.44	1.7	—
	4.5	2.4	1.3	1.1	0.28	0.52	1.1	0.48	0.40	1.6	—
	4.7	2.3	1.2	1.0	0.28	0.48	1.0	0.60	0.40	1.8	—
	5.0	2.6	1.6	1.2	0.40	0.60	1.3	0.48	0.48	2.0	—
	5.2	3.0	1.9	1.6	0.52	0.68	1.4	0.80	0.44	2.1	1.9
	5.4	3.2	2.0	1.4	0.48	0.68	1.5	0.80	0.48	2.3	2.0
	5.8	3.1	1.6	1.3	0.40	0.60	1.4	0.80	0.52	2.4	2.1
SONGS	6.4	3.6	1.9	1.6	0.52	0.76	1.6	1.0	0.60	2.6	2.4
SONGS	6.5	3.7	2.2	1.7	0.52	0.80	1.6	0.88	0.60	2.7	2.4
SONGS	8.6	4.9	2.5	2.2	0.68	1.0	2.2	1.7	0.68	3.3	3.4
8108–106.7.35	9.2	5.3	3.0	2.1	0.68	1.2	2.3	—	0.68	3.6	3.4
SONGS	9.6	5.5	2.9	2.6	0.68	1.1	2.5	2.0	0.64	3.7	3.9
8108–106.7.31	10.8	6.4	3.7	3.0	0.80	1.4	3.0	1.2	0.76	4.7	4.6
SONGS	14.3	8.6	4.3	3.7	1.0	1.6	4.2	4.0	0.96	5.8	5.3
SONGS	15.7	9.2	5.4	3.8	1.0	1.9	5.0	4.0	1.2	6.3	5.8
8108–120.25	17.0	9.5	5.8	4.2	1.2	2.0	5.4	4.2	1.2	7.1	6.9
SONGS	21.5	12.2	7.1	5.8	1.2	2.2	6.8	4.7	1.6	8.3	8.3

Developmental milestones occur at a relatively small size in *H. azurea*: notochord flexion begins at ca. 4.1–4.6 mm and is complete at ca. 5.9–6.3 mm; transformation to the juvenile occurs at ca. 10.8–14.3 mm (Fig. 7). Although spinous scales have been reported to occur in larvae of some Kyphosidae (Johnson 1984), juvenile *H. azurea*, as well as *G. nigricans* and *M. californiensis*, lack spines on their scales.

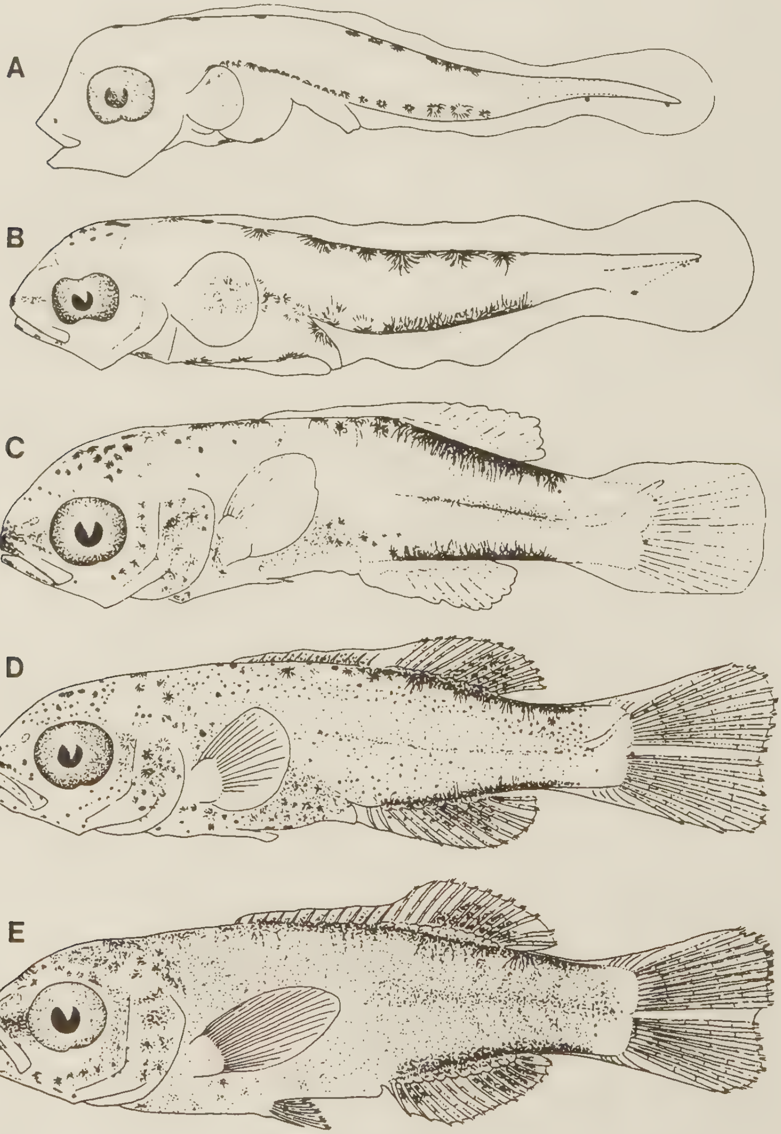

FIGURE 6.—Larvae of *Hermosilla azurea* from MEC SONGS (A–D) and CalCOFI (E) Cruises: (A) 2.6 mm NL, I–74, I–80, D–SONGS, oblique tow, 11 August 1980; (B) 4.3 mm NL, I–80, D–SONGS, surface tow, 22 September 1980; (C) 6.4 mm NL, I–53, E–LS, surface tow, 21 September 1979; (D) 8.7 mm SL, I–90, B–LS, surface tow, 27 August 1982; (E) 9.9 mm SL, 8108–NH, station 106.7.31, surface tow.

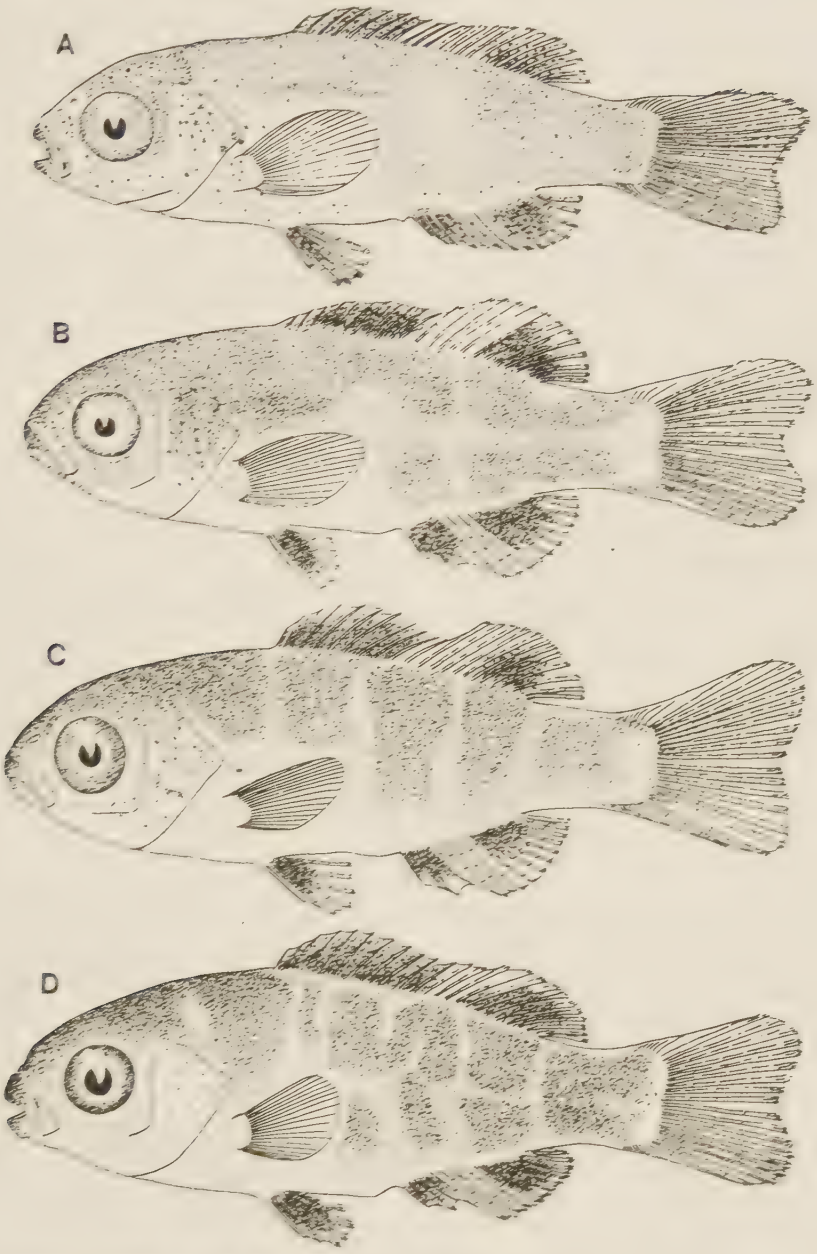

FIGURE 7.—Pelagic juveniles of *Hermosilla azurea* from MEC SONGS (A, B, D) and CalCOFI (C) surface tows: (A) 15.0 mm SL, I–35, C–1–N, 2 October 1978; (B) 16.0 mm SL, I–35, E–1–N, 2 October 1978; (C) 17.7 mm SL, 8105–NH, station 120.25; (D) 21.4 mm SL, I–35, B–1–N, 2 October 1978.

Fin Formation and Meristics

The first rays to calcify are the central principal caudal rays beginning in preflexion at about 4.1 mm (Table 7). The full complement of 9+8 principal rays is acquired during flexion at ca. 5.6 mm. Procurrent rays also may begin to calcify during flexion, as early as 5.6 mm, although more commonly they are not apparent until postflexion at ca. 6.4–6.5 mm. The full complement of 10+10 procurrent rays is completed early in the juvenile stage, by 14.3 mm.

The first dorsal and anal rays form simultaneously, early in flexion, beginning by 5.2–5.3 mm. Dorsal rays are added from anterior to posterior, with the full complement of 11 present by 5.6 mm, before the end of flexion. Dorsal spines calcify from posterior to anterior, beginning in flexion at 5.6 mm, with the full complement of 11 present in postflexion larvae by 9.4 mm. Anal rays are added from anterior to posterior, with the full complement of 10 present in flexion larvae ca. 5.3 mm long. Anal spines are added from posterior to anterior, beginning during flexion at ca. 5.6 mm; the third anal spine calcifies from the first anal ray; all three spines are present early in the juvenile stage, by 14.3 mm.

The pectoral fins initially are rounded with rounded bases, but begin to elongate during flexion when the first upper rays calcify. Addition of pectoral fin rays is from top to bottom of the fin, beginning at ca. 5.2 mm, with the full complement of 15 present by the early juvenile stage. The pelvic fins are the last to begin calcifying in the flexion stage by ca. 6.4 mm. The full complement of I, 5 rays is present by 9.4 mm.

Branchiostegal rays begin to ossify in preflexion larvae at about 4.1 mm; the full complement of 7 rays on each side is ossifying during flexion at ca. 5.2 mm. Vertebral ossification begins by 4.6 mm, just before flexion. Ossification is from anterior to posterior; all 25 centra are ossifying by the end of flexion.

Pigmentation

Preflexion larvae are relatively heavily pigmented, principally over the gut and along the dorsal and ventral midlines. In the smallest specimen examined (2.5 mm), the dorsal midline pigment consisted of a single row of 7 large stellate melanophores irregularly arranged from the midbrain to myomere 20. The number of melanophores in this dorsal row increases, so that by the beginning of flexion the dorsal and upper dorsolateral surfaces of the trunk and tail (except the last 4 or 5 myomeres) are almost completely pigmented. Dorsal and dorsolateral pigmentation on the trunk and tail becomes in-

Table 7.—Meristics of cleared and stained specimens of *Hermosilla azurea*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin rays	Anal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
2.6	—	—	—	—	—	—	—	—	—	—	—	—	—
4.1	1	1	—	—	—	—	—	—	—	—	—	—	—
4.1	—	—	—	—	2	2	—	—	—	—	—	—	—
4.6	6	5	—	—	4	4	—	—	—	—	—	—	15
4.6	6	6	—	—	5	5	—	—	—	—	—	—	15
4.6	6	5	—	—	4	4	—	—	—	—	—	—	16
4.9	4	5	—	—	4	4	—	—	—	—	—	—	16
5.2	7	7	—	—	6	6	—	—	7	8	—	—	21
5.2	6	6	—	—	5	5	—	—	—	—	—	—	20
5.3	8	8	—	—	6	6	—	—	5	8	—	—	21
5.3	8	8	—	—	6	6	—	—	10	10	—	—	22
5.6	9	8	1	1	6	6	6	6	III,11	I,10	—	—	23
6.0	9	8	—	—	6	6	8	8	V,11	II,10	—	—	25
7.4	9	8	3	3	6	6	13	12	X,11	III,10	3	3	25
9.4	9	8	6	6	7	7	15	15	XI,11	III,10	I,5	I,5	25
22.2	9	8	10	10	7	7	15	15	XI,11	III,10	I,5	I,5	25

creasingly dense and spreads posteriorly; at the end of flexion the last three myomeres are usually unpigmented but acquire pigment by the end of the larval stage.

Midbrain pigment increases in concert with the dorsal trunk and tail pigment, covering the area over the midbrain and spreading anteriorly to the snout and posteriorly over the hindbrain. Thus, by the beginning of flexion, larvae are nearly completely pigmented along the upper surface (Fig. 1H). Snout and nape pigment are usually lighter than the remaining dorsal pigment.

Preflexion larvae have a single melanophore at the roof of the mouth; during flexion more melanophores may be added in this area. A melanophore first appears below the otic capsule in the preflexion stage (by 2.6 mm) and one develops under the anterior midbrain by 3.1 mm. Melanophores proliferate in these areas to give the appearance of a stripe through the head by, or during, flexion.

Pigment first appears on the dorsal surface of the hindbrain by 2.8 mm (one melanophore), and rapidly increases to essentially cover the dorsal surface of the hindbrain by early flexion (ca. 4.8 mm). This pigment subsequently extends posteriorly as a series of melanophores over the vertebral column.

One or two melanophores first appear at the tip(s) of the upper and/or lower jaw(s) between 2.8 and 3.1 mm. Melanophores spread along the upper jaw beginning late in preflexion or early in flexion, and along the lower jaw beginning midway or later through flexion. At ca. 2.8 mm a single melanophore appears on the gular membrane; by the beginning of flexion 3–4 additional melanophores form a longitudinal series evenly spaced along the membrane (Fig. 1G).

A single melanophore appears on the opercle late in preflexion or early in flexion (by 4.4 mm). Melanophores proliferate here to form a large pigment patch midway through flexion, and subsequently extend dorsally, ventrally, and anteriorly to cover the entire opercular area, usually by the end of flexion or early in postflexion.

The smallest specimens examined had a continuous double row of melanophores, which extended over the dorsal surface of the gut and swimbladder, and posteriorly as a single row nearly to the end of the hindgut. These specimens also had 1–6 melanophores evenly spread along the ventral midline of the gut from the anterior midgut to the anterior hindgut. The dorsal gut pigment increases, extending as far as halfway down the front and sides of the gut by the beginning of flexion, and completely covers the sides of the gut by the end of flexion. This pigment continues to spread ventrally, from anterior to posterior, meeting the midline series in postflexion larvae (between 8.6 and 9.6 mm). The series of melanophores along the ventral midline of the gut changes little during larval development. Modal numbers of melanophores in the series were 3–4 (range of 1–6) for preflexion larvae and 4 (range of 2–6) for flexion larvae.

Initially, ventral midline pigment on the tail consists of a single row of 7–10 large melanophores between the first and the 13th postanal myomeres. Usually 2 or 3 (1–4) small melanophores lie under the notochord tip; later these become located along the hypural margin (Fig. 6B, 6C). Occasionally, the first one or two postanal myomeres are unpigmented in preflexion larvae (14% of the preflexion specimens lacked pigment here), but thereafter the first postanal myomeres are always pigmented. The ventral melanophores enlarge and may increase in number during preflexion, so that by ca. 3.5 mm a melanistic band extends along the tail to ca. myomere 20 or 21.

A series of 1–3 small melanophores appears on the lateral midline of the tail at the 14th–20th myomeres late in preflexion or early in flexion (ca. 3.7–4.3 mm). Melanophores proliferate to form a band as do the ones along the dorsal and ventral midlines. Further enlargement of the ventral, lateral, and dorsal bands results in a nearly continuous tail bar during mid to late flexion. Subsequent proliferation of melanophores in this region and over the gut and trunk results in complete body pigmentation, except for the last 3–5 myomeres, by ca. midway through postflexion. Pigmentation is complete by transformation.

The dorsal and ventral midline pigment begins to spread onto the bases of the middle and posterior dorsal and anal soft rays during flexion at ca. 5.4 mm. By late flexion or early postflexion the membranes between dorsal rays 5 or 6 to 10 or 11 and between anal rays 5, 6 or 7 to 9 or 10 are pigmented. During postflexion, the base of the entire dorsal fin becomes heavily pigmented and near the end of the larval stage the membranes between the dorsal spines become pigmented (by ca. 9.6 mm). Pigmentation does not develop on the membranes between dorsal soft rays 1–5 during the larval period, and is very sparse there in juveniles. The base of the entire anal fin is pigmented by 8.6 mm; the anal spines and membranes are heavily pigmented by 9.6 mm, as are the membranes between anal soft rays 5 to 9 or 10. The membranes between anal soft rays 1–5 are usually unpigmented in larvae, and only sparsely pigmented in juveniles.

Caudal fin pigment is usually restricted to the melanophore(s) at the distal hypural margin during the larval stage. Small melanophores may be acquired along the proximal edges of some of the principal caudal rays in small juveniles.

The first pigment on the paired fins consists of a single melanophore on the lower proximal external surface of the pectoral fin base. This melanophore may appear as early as 4.8 mm, but is not consistently present before ca. 8.6 mm. Pectoral pigment subsequently changes little, except that beginning at ca. 9.6 mm, melanophores appear at the bases of the upper pectoral rays. The pelvic fins are unpigmented in larvae but become heavily pigmented in small juveniles.

Transforming specimens are uniformly pigmented except for the residual melanistic bands at the dorsal and ventral margins and along the lateral midline of the tail. Between 11 and 14 mm, a series of faint bars begins to appear, one anterior to the dorsal fin, one below the spinous dorsal, one below the transition from spinous to soft dorsal, one below the soft dorsal, and one at the caudal peduncle (Fig. 7C). The bars are usually interrupted along the lateral midline and variously developed below the midline, giving a mottled appearance. The mottled appearance is intensified when the bars begin to subdivide and ultimately produce the 12 bars found in late juveniles and adults.

DISTRIBUTION

Girella nigricans

A total of 71 occurrences of *G. nigricans* larvae were recorded from CalCOFI oblique plankton tows during the period 1951–81 (Fig. 8). Larvae were not found on survey cruises during 1951, 1953, 1955, and 1972. Identification of some shorefish species was of variable competency during the early years of CalCOFI and this may explain the apparent absence of *G. nigricans* larvae in 1951, 1953, and 1955. Larvae ranged from San Luis Obispo, CA (cruise 6907, station 77.48) to San Cristobal Bay, Baja California (cruise 5810, station 137.23)—the former station is the only record north of Pt. Conception, CA. Thirty-eight percent of the total occurrences were between Pt. Conception and the Mexican border and 62% were off Baja California. Larvae ranged seaward to ca. 330 km (cruise 6407, station 93.70); however, 80% of the occurrences were from station 40 shoreward on the CalCOFI survey lines (typically <110 km from the coast). Numbers of larvae sorted from each sample were low, ranging from 1 to 5, with a mean of 1.35 per positive tow. The standardized mean number per positive tow was 4.0 with a range of 0.3–17.5[1]. *Girella nigricans* is a highly seasonal spawner with 80% of the larvae occurring in summer months (June, 27%; July, 45%; August, 8%). Larvae were not taken in January–March.

The importance of the surface layer as a habitat for *G. nigricans* larvae has not been assessed; however, the addition of surface (Manta net) tows on CalCOFI stations during the 1978 and 1981 surveys has provided some information. Larvae occurred in nine surface tows in 1978 and in 11 tows during 1981. These occurrences compare with those from three positive oblique tows in 1978 and one in 1981 and suggest that 1) *G. nigricans* larvae may occur frequently in the neuston and 2) they are undersampled by oblique tows. The mean size of larvae taken in surface nets is nearly twice that of larvae taken in oblique tows. The mean larval length from surface tows during 1978–81 was 7.1 mm ± 3.7 SD (range = 2.6–16.5 mm). The mean for oblique tows during 1978–81 was 3.8 mm ± 1.69 SD (range = 2.2–15.0 mm).

Medialuna californiensis

A total of 150 occurrences of *M. californiensis* larvae were recorded on CalCOFI oblique plankton tows during 1951–81 (Fig. 8). Larvae occurred on all surveys except during 1953; the apparent absence during 1953 probably was a result of identification error. Larvae ranged from off Monterey Bay, CA (cruise 5707, station 67.55) to off Pt. San Jaunico, Baja California (cruise 6507, station 133.50). There were only five occurrences north of Pt. Conception, CA, during the 30 yr period; only one of these was near the coast (Fig. 8). Except for two stations,

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[1] Standardized number adjusts for percent of sample sorted and standard haul factor to give the number of larvae under 10^2 m of sea surface (see CalCOFI ichthyoplankton data reports cited in Ambrose et al. 1988).

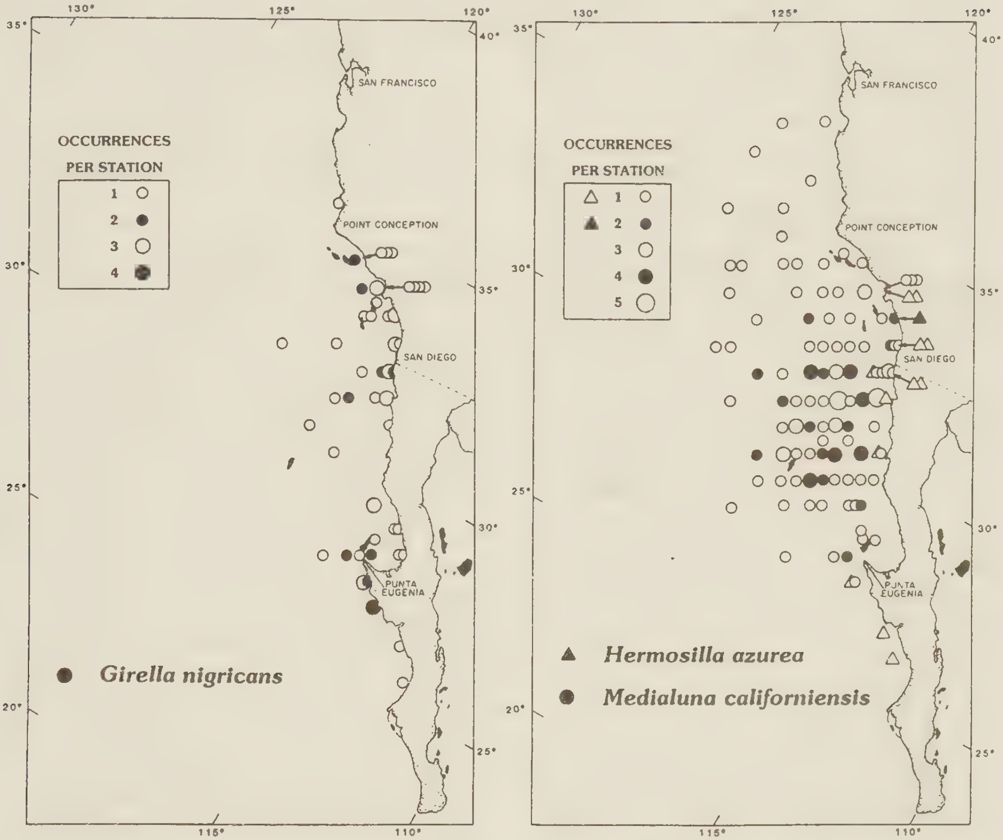

FIGURE 8.—Pooled numbers of occurrences of *Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea* larvae taken in CalCOFI tows from 1951 to 1981. Occurrences for *G. nigricans* and *M. californiensis* represent oblique tows and those for *H. azurea* are both oblique and surface tows.

all the remaining larvae were taken between Pt. Conception, CA and Pt. Eugenia, Baja California; 28% of these occurrences were off California and the remainder were off Baja California.

In contrast to *G. nigricans* larvae, those of *M. californiensis* occur well offshore to a distance of ca. 500 km (cruise 5505, station 93.95); 71% of the occurrences were seaward of Station 40 (>110 km from the coast on most lines). Numbers of larvae ranged from 1 to 11 with a mean of 1.42 per positive tow, slightly higher than for *G. nigricans*. The standardized mean number per positive tow was 4.94 with a range of 1.0–30.7. Like *G. nigricans*, the occurrence of *M. californiensis* larvae was highly seasonal with 53% taken in July and 90% in June–August. Larvae did not occur in November–March.

Larvae of *M. californiensis*, like those of *G. nigricans*, utilize the neuston habitat and may be undersampled by oblique tows. *Medialuna californiensis* occurred only once in the oblique tows during 1978 and once in 1981, whereas there were five positive Manta tows in 1978 and three in 1981. The mean size of larvae taken in surface tows during 1978–81 was almost twice that in the oblique tows (7.0 mm ± 2.60, range = 2.6–11.0 mm versus 3.9 mm ± 1.18, range = 2.3–9.4 mm).

Hermosilla azurea

Larvae of *H. azurea* have a nearshore shallow distribution (Fig. 8). We can document only two occurrences of this species in the entire CalCOFI time series of oblique tows (cruise 6907, station 93.30, two specimens; station 97.29, four specimens). Since this species was first identified during the course of the present study, it is possible that other misidentified specimens reside in the collections. They were not, however, confused with *G. nigricans* or *M. californiensis* since we have reexamined all identifications of these species. Larvae of *H. azurea* occurred in Manta net samples at three stations during the 1978 survey and at nine stations on the 1981 survey. Occurrences ranged from Santa Monica Bay, CA (cruise 8107, station 86.7.33) to Pt. San Juanico, Baja California (cruise 7807, station 133.23). Occurrences were shoreward of station 36 on each CalCOFI line (4–42 km from the coast).

Larvae of *H. azurea* were well represented in the SONGS plankton collections of MEC Analytical Systems. The shallow distribution of *H. azurea* larvae was clearly demonstrated in the SONGS collections. Surface tows accounted for 87% of the larvae and oblique tows for 14%. Larvae occurred principally in the outer section of the SONGS transect (1.9–7.2 km from the coast; ca. 18–75 m depth). Larval occurrence was highly seasonal, with 62% of the total number taken in August and >99% in July–September.

SYSTEMATICS

Johnson (1984) discussed kyphosid fishes in his review of percoid systematics and ontogeny. He considered Girellidae, Kyphosidae, and Scorpididae to be distinct families and redefined the latter to include only four genera (*Scorpis*, *Medialuna*, *Labracoglossa*, and *Bathystethus*). Evidence from adult anatomy that led to these decisions was deferred to a forthcoming review (Johnson and Fritzsche, in press). Johnson (1984) pointed out the similarity of girelline and scorpidine larvae and presented this as evidence for considering them sister groups; he now believes girellines, scorpidines, and kyphosines form a monophyletic group (G. D. Johnson[2]).

A principal problem in assessing ontogenetic characters of teleost fishes is a lack of information for all but a few taxa under consideration. This is especially true for percoids and for this group of percoids. In addition to our description of *Girella nigricans*, ontogenetic series are known for two other species of *Girella* (*G. punctata* eggs, larvae, and juveniles [Mito 1958a]; *G. melanichthys* larvae [Okiyama 1988]). Developmental stages of the other girelline genus (*Graus*) are unknown. Other than our description of *Medialuna californiensis*, the only scorpidine larval series description is that of *Labracoglossa argentiventris* (Hattori 1964). Developmental stages of two of the four kyphosine genera are known. In addition to our description of larvae and pelagic juveniles of *Hermosilla azurea* there are descriptions of developmental stages of at least three species of *Kyphosus* (*K. cinerascens* larvae and juveniles, [Mito 1958b; Okiyama 1988]); *K. sectatrix* transforming larvae and juveniles [Moore 1962]; *K. incisor* transforming larvae and juveniles [Moore 1962]; *K. vaigensis* or *bigibbus* eggs [Watson and Leis 1974]; *K. vaigensis* or *bigibbus* larvae [Miller et al. 1979; Leis and Rennis 1983]). Developmental stages of *Sectator* have not been described.

The literature on development stages of these fishes does not provide sufficient descriptive detail to adequately assess ontogenetic characters. In this paper we present detailed descriptions of representatives of the three putative families to establish a basis for character comparisons. The striking feature of the three larval series is their similarity. The fact that the three species were confused with one another during the history of CalCOFI surveys attests to this in a practical sense. Our more rigorous study of their morphologies and pigment patterns has allowed us to identify each specimen correctly, while reinforcing the similarities perceived by early CalCOFI workers. These similarities are 1) a general percoid body form with a *Girella-Medialuna-Hermosilla* grade in degree of robustness; 2) dorsal and ventral midline melanophore series, with unique variations for each species; 3) lateral midline melanophore series, with unique variation; 4) an embedded melanistic band through the eye region; 5) minute melanophores at the tip of the notochord which become associated with the hypural margin of the caudal fin; 6) an anteriad progression of general body pigmentation late in the larval period; and 7) head spination with a *Girella-Hermosilla-Medialuna* grade in degree of development. This morph is not unique among percoids (see Leis and Rennis 1983; Johnson 1984); however, the coherence of these and other more subtle characters among these three eastern Pacific species supports the argument that they represent sister groups.

The pattern of lateral pigmentation is more variable in kyphosine larvae than in girellines and scorpidines. We can recognize three patterns of lateral body pigment in kyphosines. The pattern in *H. azurea* larvae is essentially like that in *Girella* and *Medialuna*. It begins as a midlateral series on the tail and fills in the unpigmented region above, below, and anteriad to it. In *Kyphosus sectatrix* and *K. incisor* lateral pigment extends along the entire epaxial region of the body (Moore 1962). In *K. cinerascens* and *K. vaigensis* (*bigibbus*?) larvae a broad zone of lateral body pigment expands to cover unpigmented regions above, below, anteriad, and posteriad to it (Mito 1958b; Leis and Rennis 1983).

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[2] G. D. Johnson, Fishery Scientist, National Museum of Natural History, Washington D. C. 20560, pers. commun. April 1989.

Ontogenetic divergence among kyphosid fishes is greater during the pelagic juvenile stage than in larvae. The silvery pelagic juveniles of *Girella*, which transform abruptly to olive benthic juveniles, are well known. Apparently, *Medialuna* not only has a silvery pelagic juvenile too, but also has a strongly variegated pattern on the dorsal and anal fins. The pelagic juveniles of *H. azurea* are strongly mottled. This feature is shared with other kyphosines, some of which exhibit a striking pattern of pale spots (*K. sectatrix* and *K. incisor* [Moore 1962]; *K. cinerascens* [Mito 1958b]; *K. vaigensis* (*bigibbus*?) [W. Watson, pers. obs.]).

Ontogenetic stages of kyphosid fishes provide a promising array of systematic characters. The utility of these characters in assessing phylogenetic relationships is limited by our present inability to identify shared derived character states through outgroup comparison. The solution to this problem awaits a broader knowledge of ontogeny in kyphophids and other groups in the percoid series.

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Beginning with this issue, there is a new size, cover, and design of the *Fishery Bulletin*, the first major change since 1971. The new effect was designed by Harold Spiess, Visual Information Specialist in the Scientific Publications Office, National Marine Fisheries Service, NOAA, with guidance from the Managing Editor, Mary S. Fukuyama, in coordination with NMFS Scientific Editor, Dr. Andrew E. Dizon.

8974

Midgut Cell Height Defines Nutritional Status of Laboratory Raised Larval Northern Anchovy, *Engraulis mordax*

Gail H. Theilacker and Yoshiro Watanabe

ABSTRACT: The height of the midgut mucosal cells was developed as a diagnostic index to assess the past feeding history of larval northern anchovy and to estimate starvation mortality of larval fishes in the sea. The index was compared to traditional histological indices and tested for field use. The height of the mucosal cells was a sensitive index, yielding reliable estimates of larval condition. Because it was sensitive, easy to measure and dependable in formalin-fixed tissue, this diagnostic index should be useful and practical for field work. Additionally, unlike other diagnostic criteria, it resisted the effects of autolysis (withstood prolonged time in the collecting net). Also included is a discussion of the growth characteristics of northern anchovy larvae that experienced a delay in feeding.

Larval mortality may determine recruitment of young fish to a fish stock. A major cause of larval mortality is starvation (Hunter 1976a; Lasker 1981). Several techniques have been recently developed to estimate the proportion of natural mortality caused by starvation. A histopathological technique that uses cellular criteria to identify larval nutritional condition was calibrated in the laboratory (O'Connell 1976; Theilacker 1978; Martin and Malloy 1980), applied to field studies to yield assessments of larval nutritional condition (O'Connell 1980; Theilacker 1986; Margulies 1986; Setzler-Hamilton et al. 1987), and successfully used to estimate rates of starvation-induced mortality (Theilacker 1986). Another technique that employs a morphometric approach generated good predictions of nutritional condition for several larval fish species (Theilacker 1978, 1986; Martin and Malloy 1980; Martin and Wright 1987; Setzler-Hamilton et al. 1987) as did the use of an RNA/DNA index (Buckley 1979; Wright and Martin 1985; Clemmesen 1987; Buckley and Lough 1987; Setzler-Hamilton et al. 1987).

Each of these diagnostic techniques suffers from various constraints. To develop histological criteria, an accurate representation of the structure of live tissue is needed for identifying larval fish condition. The usefulness of these criteria depends on the tissue quality of the field-collected specimens. For many fishes (northern anchovy and striped bass, *Morone saxatilis* (O'Connell 1980; Setzler-Hamilton et al. 1987)), autolytic tissue decomposition occurs within 2–3 minutes after sampling. Because routine ichthyoplankton collections usually take 21 minutes (Smith and Richardson 1977), special plankton collections are required for histopathology. Additionally the routine solution (3–5% formalin) used to preserve plankton does not adequately preserve cellular structure of larval fishes and special solutions (Bouin's fixative) must be used (O'Connell 1976; Theilacker 1978). The morphometric analysis requires extensive calibration studies to estimate the effect of the net and preservatives on shrinkage of body parts because the morphometric indices are very sensitive to shrinkage (Theilacker 1980; 1986). The RNA/DNA index must be calibrated for temperature effects and animal age (Ota and Landry 1984; Buckley 1984; Buckley and Lough 1987); however, there are other considerations that may limit its application. Furthermore, RNA/DNA is generally regarded as an index of potential growth (protein synthesis rates) not starvation mortality.

In March of 1985, we anticipated applying the histopathological technique developed by O'Connell (1976) to estimate starvation rates of northern anchovy collected at two sites off the coast of California (see Owen et al., 1989). However, when aboard ship, we found that it was impossible to preserve the larvae within the required 2–3 min time period (needed to maintain tissue quality) and take a sample that was representative of the zone inhabited by larval anchovy. We were unable to use the established histological criteria because it took us 5 or more minutes to sample larval anchovy from 50 m to the surface and process our collection. Thus, to estimate anchovy starvation rates, we needed to develop

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new criteria that were stable for a longer period.

Here we describe and evaluate a diagnostic index, the height of midgut mucosal cells of larval northern anchovy. The index is sensitive to feeding history, resistant to autolysis (withstands prolonged time in a collecting net), and simple to measure. It is reliable for fish fixed in formalin, the commonly used fixative for field collections.

METHODS

Experimental Design

We raised larval northern anchovy under different feeding conditions to produce specimens that exhibited various health states. These larvae were used to describe growth, determine the dominant midgut height measurement within each feeding treatment, evaluate the midgut index, and estimate response times. In a second series of experiments, groups of fed and starved fish were treated with nets in a manner designed to simulate plankton collection methods in the sea. These studies were used to evaluate how useful the new criterion would be in a field situation.

Rearing Treatments

Five groups of anchovy were raised at 15.5°C for three weeks in 100 L containers. The eggs, stocked at 10/L, were collected from a hormone-injected broodstock maintained at the Southwest Fisheries Center aquarium (Leong 1971). We fed the control group ad libitum on *Gymnodinium* and *Brachionus* (Lasker et al. 1970; Theilacker and McMaster 1971) at yolk absorption (four days after hatching at 15.5°C; hatching = day 0), and delayed feeding 1–4 days in the other groups. Fish were sampled daily from the fed, starved, and delay-fed treatments and preserved in Bouin's fixative (Table 1).

Field Simulation Experiments

One group of northern anchovy was fed for 3 days and one was starved for 3 days. We treated samples from each group of 7 d old fish in a net by flushing the submerged net with 15.5°C seawater for 0, 2, 5, 10, 15, 20, and 25 minutes (see Theilacker 1980 for details of this method). After the net treatment, fish were preserved in either 5% buffered formalin (standard shipboard fixative) or Bouin's solution (required fixative for histopathology).

Histological Preparation

We measured the standard length (SL) of preserved larvae to the nearest 0.01 mm and subsequently prepared them for histopathology using standard microtechniques (O'Connell 1976). Tissue was dehydrated, embedded in paraffin, serially sectioned at 6 µm in the sagittal plane, mounted, and stained with hematoxylin and eosin.

Measurement of Midgut Cell Height

The midgut is the major part of the intestine of

TABLE 1.—Standard length (SL) and

	Fed					
	Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ µm
4	FED					
5	32	3.95	0.23	10	3.93	19.63
6	34	3.92	0.21	17	3.87	20.13
7	26	4.33	0.24	13	4.29	19.52
8	33	4.59	0.46	19	4.67	19.13
9	33	5.29	0.40	10	5.26	22.13
10	38	5.54	0.33	10	5.85	21.88
11	26	6.22	0.47	10	6.09	21.13
12	55	6.36	0.48	10	6.52	20.75
13	38	6.85	0.43			
14	36	7.20	0.54			
17	66	7.22	0.74			
19	35	7.43	0.80			
Total *n*	452			99		

	Starved 3 d/fed					
	Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ µm
4	STARVED					
5	STARVED					
6	STARVED					
7	28	3.37	0.22	13	3.29	10.19
8	25	3.35	0.15	13	3.35	9.90
9	29	3.79	0.24	10	3.83	11.38
10	26	3.90	0.25	17	3.93	12.28
11	36	3.92	0.19	11	3.96	14.21
12	34	4.00	0.35	10	4.00	14.88
13	31	4.25	0.38			
14	26	4.63	0.41			
17	31	5.27	0.45			
19	30	5.51	0.68			
24	34	6.80	0.90			
Total *n*	330			74		

[1] SL taken on Bouin's fixed larvae
[2] Midgut cell height (see text)

larval northern anchovy; it extends from behind a constriction at the pylorus to another constriction at the beginning of the hindgut (Fig. 1). We measured the cell heights under a light microscope using the histological preparations. Epithelial cells of the midgut tend to decrease in height from the anterior part to the posterior end. We chose the midpart of the midgut (from 2/5 to 3/5 of the entire length) as the measurement site. The area is easily located in histological sections that are cut parallel to the median plane. The dorsal and ventral rows of midgut cells appeared in these sections. We measured the cells of the ventral row that were larger than the dorsal row, probably because of greater absorptive activity. We selected a section having four to six neighboring cells in which the nuclei, brush border, and cell base were clearly defined; brush border may be indistinct in larvae of poor condition. Measurements were taken from the luminal surface of the brush border to the cell base delimited by a basement membrane, using a micrometer attached to an eye lens. Usually, in sagittal sections, the cell heights are not so varied within the middle part of the midgut. If, however, there were slight differences between cells due to a slight angle of the section, we took an average of several measurements.

midgut cell height (mght) statistics for fed northern anchovy by diet and age.

	Starved 1 d/fed						Starved 2 d/fed					
	Growth			Midgut			Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ µm	*n*	SL[1] $\bar{x}$ mm	SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ µm
4	STARVED						STARVED					
5	33	3.55	0.20	12	3.95	14.27	STARVED					
6	47	3.59	0.37	15	3.60	15.83	27	3.58	0.22	18	3.57	13.47
7	61	3.46	0.23	11	3.45	14.89	33	3.39	0.18	10	3.35	11.88
8	23	3.81	0.31	10	3.77	16.00	31	3.58	0.21	17	3.60	12.21
9	49	4.34	0.46	11	4.79	19.32	18	4.07	0.21	10	4.02	14.63
10	46	4.90	0.39	10	4.80	18.63	38	4.25	0.32	11	4.19	14.77
11	55	5.09	0.56				41	4.58	0.31	10	4.60	15.63
12	71	5.56	0.47				28	4.95	0.39			
13	47	5.86	0.45				27	4.99	0.41			
14	61	6.32	0.62				46	5.63	0.45			
17	121	6.84	0.86				33	6.25	0.73			
19	26	7.19	0.95				39	6.65	0.93			
Total *n*	640			69			361			76		

	Starved 4 d/fed					
	Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ µm
4	STARVED					
5	STARVED					
6	STARVED					
7	STARVED					
8	19	3.40	0.19	10	3.44	10.51
9	14	3.58	0.22	6	3.59	10.00
10	6	3.66	0.12	6	3.66	8.13
11						
12						
13						
14						
17						
19						
24						
Total *n*	39			22		

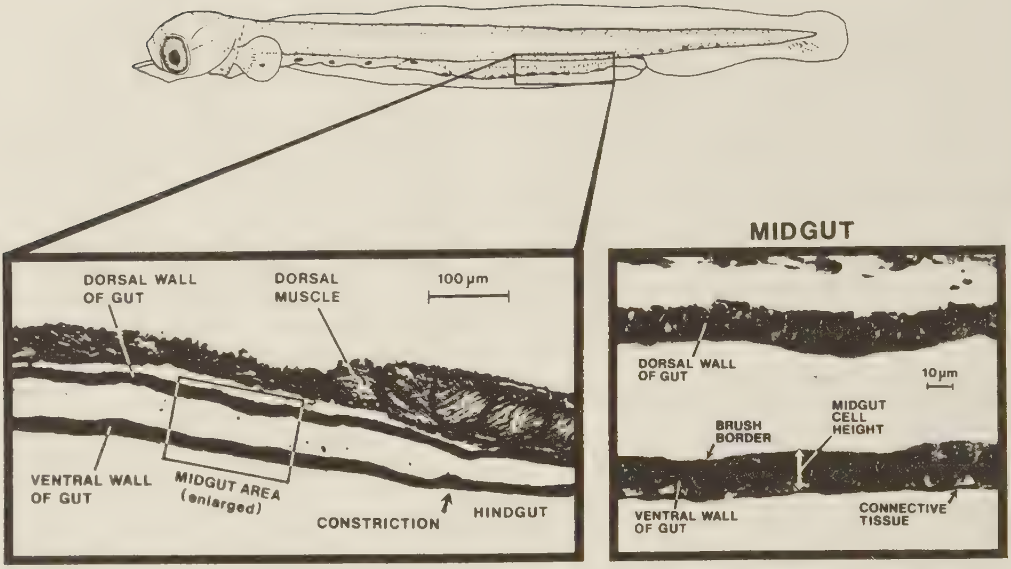

FIGURE 1.—*Engraulis mordax* larva showing measurement site for midgut cell height.

Evaluation of Midgut Criteria

To evaluate the capacity of the midgut cell height measurement to classify larval anchovy condition, we graded 5–10 larvae taken daily from 3 treatments (fed, feeding delayed 1 day, and starved) using both O'Connell's (1976) histological criteria and the midgut cell height. We assumed that the histological criteria (the sum of the cellular grades for the brain, cartilage, notochord, musculature, liver, and midgut) would yield the best estimate of larval condition, and we compared the power of each index to predict past feeding history.

RESULTS

Diet-Induced Differences in Growth

Growth of the fed control group was 0.41 mm/d, similar to published reports for northern anchovy raised in the laboratory (Kramer and Zweifel 1970; Hunter 1976b; Theilacker 1987). Larvae experiencing a feeding delay of 1, 2, and 3 days were smaller at 10.8 days than larvae not experiencing a delay, and as the starvation interval increased, their final size decreased (Table 2). For the test of significance of size at age, P was <0.01 for all delay combinations except the starved 3 d/fed (S3/F) vs. the 4 d delay in feeding

TABLE 2.—Diet-induced differences in growth of northern anchovy at a common age and at a common feeding period (n's for common feeding period slightly less than n's for common age).

	Common age				Common feeding period		
Diet	n	Age d	Feeding period d	SL $\bar{x}$ mm	Age d	Feeding period d	SL $\bar{x}$ mm
Fed	452	10.8	6.8	5.58	10	6	5.51
Starved							
1 d/fed	640	10.8	5.8	4.87	11	6	4.96
2 d/fed	394	10.8	4.8	4.48	12	6	4.75
3 d/fed	372	10.8	3.8	4.00	13	6	4.32
4 d/fed	114	10.8	2.8	3.98	—	—	—

(S4/F) where $P = 0.8$, indicating that delaying feeding affected the final fish size at a given age (ANOVA; Table 2).

Progressively increasing the periods of starvation before feeding also caused a decrement in the growth rate after feeding resumed (Fig. 2; Table 2). Larvae were unable to compensate for a delay in feeding at the onset, and fish length at an age where all fish had been feeding for 6 days differed for each treatment [$P = < 0.01$ for all diet combinations except starved 1 d/fed (S1/F) vs. 2 d delay in feeding (S2/F) where $P = 0.08$ (ANOVA; Table 2)]. Growth rates for the 6 d period ranged from 0.41 mm/d for the fed group, 0.39 mm/d for 1 d delay in feeding (S1/F), 0.34 mm/d for 2 d delay (S2/F), 0.31 mm/d for 3 d delay (S3/F). Length was transformed to natural logs for the ANOVAs. The test for the equality of slopes showed that all slopes differed ($P = < 0.0001$ for all combinations). Thus, delaying feeding affected the final fish size and caused a decrement in the growth rate after feeding resumed.

Evaluation of Midgut Cell Height Criterion

For a subset of northern anchovy larvae taken from the treatments where larvae were fed, starved, and feeding was delayed 1 day (S1/F), we compared the number of larvae correctly classified to feeding treatment by the midgut cell height and by the traditional histological index (O'Connell 1976). To define the midgut cell height interval for each feeding treatment, we selected the midpoint between successive cell height means (Table 3) as the interval breakpoint for predicting feeding history from cell height. The midgut cell height was correlated with the histological score (Fig. 3, $n = 38$, $P < 0.001$, t-ratio = 25.85). Both the cell height and the histological score correctly classified all of the subset larvae that were fed to the correct group and 78 and 79% of the starved larvae to the correct group. On the other hand, for the delayed feeding group (S1/F), the midgut cell height was a better predictor of feeding history than the histological score. The midgut measurement classified 78% correctly whereas the histological score classified only 50% correctly.

After the apparent success of this evaluation, we used the midgut cell height data set (Table 1; Fig. 4) to establish the criteria needed to define and calibrate the midgut cell height measurement for predicting feeding history and for calculating starvation rates of anchovy larvae in the sea.

Diet and Midgut Cell Height Categories for Larvae <4.0 mm

We defined the diet and cell height categories for first-feeding larvae (<4.00 mm SL) which are vulnerable to starvation. The height of the

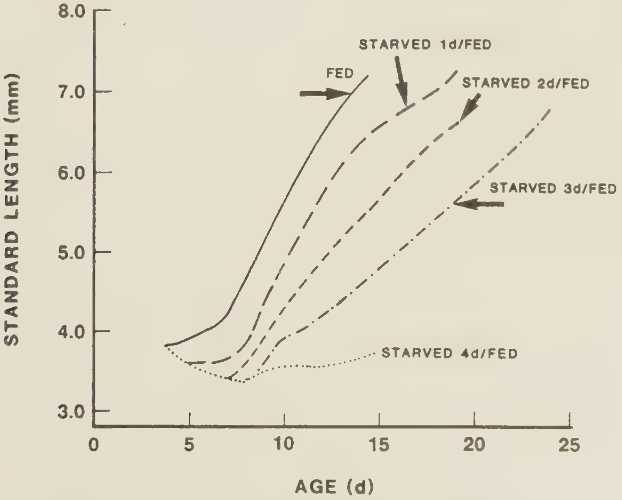

FIGURE 2.—Growth of *Engraulis mordax* larvae under different feeding conditions.

TABLE 3.—Midgut cell height (mght) statistics for six diets by northern anchovy size.

Size Interval (mm)	Fed n $\bar{x}$ mght (μm) SD	Starved 1 d/fed n $\bar{x}$ mght (μm) SD	Starved 2 d/fed n $\bar{x}$ mght (μm) SD	Starved 3 d/fed n $\bar{x}$ mght (μm) SD	Starved 1 & 2 d n $\bar{x}$ mght (μm) SD	Starved 3 & 4 d n $\bar{x}$ mght (μm) SD	All
<4.00	20	31	33	41	28	24	176
	20.50	15.56	12.58	11.77	13.48	10.38	
	2.27	3.18	2.12	2.44	2.81	2.00	
4.00–4.99	40	18	27	20			105
	19.47	17.36	15.28	13.68			
	3.67	3.58	2.51	2.64			
5.00–5.99	21	8					29
	20.95	20.63					
	2.71	3.78					

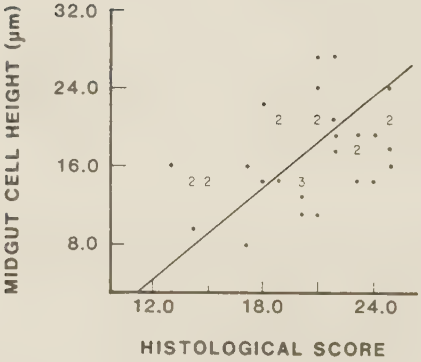

FIGURE 3.—*Engraulis mordax* larvae, regression of midgut cell height measurement on histological score.

midgut cells decreased from the fed to the starved state. The average height of the midgut cells in fed fish <4.00 mm was 20.5 μm. The height averaged 15.6 μm when feeding was delayed one day, 12.6 μm for a 2 d delay and 11.8 μm for a 3 d delay in feeding. The mean midgut height for larvae starved 1 and 2 days was 13.5 μm and for the 3 and 4 d starved group was 10.4 μm (Table 3; Fig. 5).

The height of midgut cells of the fed group (fed) and those where feeding was delayed 1 day (S1/F) was different from all other groups (ANOVA P's < 0.01; Table 4). Fish starved 3 and 4 days (S3&4) also differed from all others (P's < 0.05 level). On the other hand, midgut cell heights of larvae starved 1 and 2 days (S1&2) were not different from those of larvae in which feeding was delayed 2 or 3 days (S2/F and S3/F) (P's = 0.16 and 0.17; Table 4). The t-test matrix indicated four distinct diet and cell height

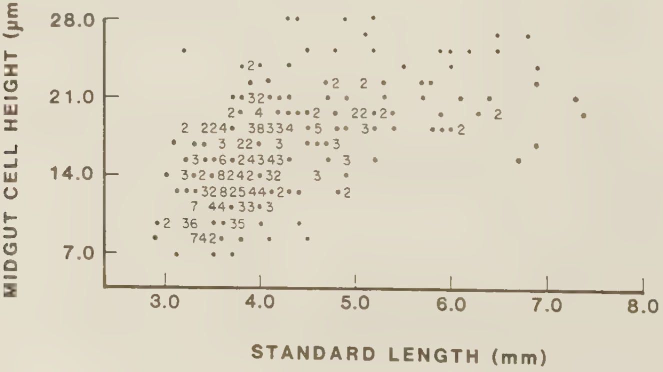

FIGURE 4.—Midgut cell height measurements for *Engraulis mordax* larvae that were raised in the laboratory. Fish were either fed, starved, or feeding was delayed.

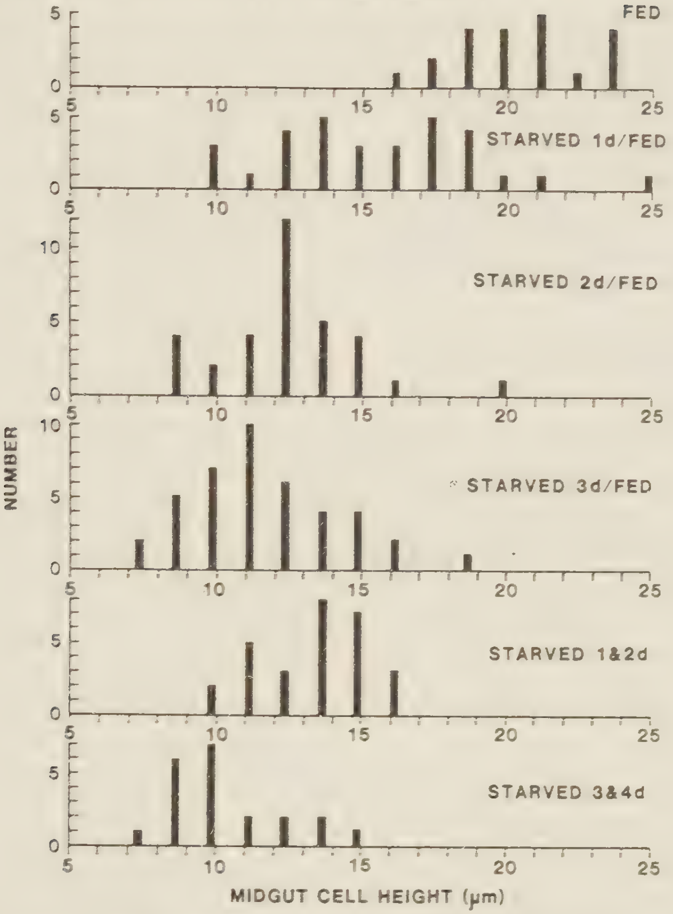

FIGURE 5.—Midgut cell height measurements for *Engraulis mordax* larvae <4.00 mm raised using various feeding conditions.

TABLE 4.—Paired comparison of midgut cell heights for six diets for northern anchovy <4.00 mm SL: *t*-test matrix and probabilities ($P = < 0.01$, **; $P = < 0.05$, *; $P = > 0.05$, value)

		Starved				
	Fed	1 d fed	2 d fed	3 d fed	1 & 2 days	3 & 4 days
Fed	0.0000					
Starved						
1 d fed	− 6.8438**	0.0000				
2 d fed	−11.1211**	−4.7522**	0.0000			
3 d fed	−12.7320**	−6.3433**	−1.3731 .17	0.0000		
1 & 2 days	− 9.5331**	−3.1765**	1.4029 .16	2.7802**	0.0000	
3 & 4 days	−13.1632**	−7.4916**	−3.2143**	−2.1187*	−4.3834**	0.0000

categories for first-feeding larvae: 1) a fed category, 2) a category for 1 d delay in feeding (S1 F), 3) an intermediate category (S2 F + S3 F + S1&2), and 4) a starved category (S3&4).

Calibrations for Field Studies

To estimate daily starvation rates in the sea using cell height, an approximation of the duration or response time for each size, diet, and cell height category is needed. The duration is the number of days that larvae belonging to the size, diet, and cell height category remain within that category. Daily rates in the sea (estimates of numbers of larvae per day) are determined by dividing the number of field-collected larvae classified to each category by the category duration. See the following section on "Applying the Calibration Criteria" for a more detailed explanation of this procedure.

Duration for Fed Category, <4.00 mm SL

Fed larvae began to eat at 3.8 mm (preserved length), yet there was little or no growth for 2 days (Fig. 2). Even though, on the average, the fed anchovy grew at 0.41 mm/d, when the delay in growth was considered, the resulting duration for the <4.00 mm fed group was 2.5 days. Thus it took 2.5 days for the fed fish to move out of this size, diet, and cell height category. This initial lag in growth was reported earlier for northern anchovy (Theilacker 1987).

Durations for Intermediate Categories, <4.00 mm SL

The durations were 5 days for diet groups where feeding was delayed 1 and 2 days (S1/F and S2/F). The group that was starved 3 days before feeding (S3/F) remained within the midgut cell height interval for 8 days (Table 1). The duration for larvae that were starved for 1 and 2 days (S1&2) was 2 days.

Duration for Starved Category, <4.00 mm SL

The duration for the group starved 3 and 4 days (S3&4) was 2 days. Northern anchovy larvae died after starving 3–4 days. No larvae belonging to the starved category were larger than 4.0 mm.

Field Feasibility Study

Because larval fish tissues decompose rapidly due to autolysis (Theilacker 1978; O'Connell 1980), we tested the effects that the prolonged processing periods encountered at sea have on the integrity of the midgut cells. In this study, after 5 minutes in the net, the condition of both formalin- and Bouin's-fixed larval tissues could not be graded using traditional histological criteria due to indistinct nucleoli, diffused nuclei, and intercellular spaces. However, measurement of midgut cell height was still possible after 25 minutes.

The height of the midgut cells, whether measured in formalin- or Bouin's-fixed individuals, showed little change in height over the 25 min processing period (Fig. 6a–d; slope b is not significant from 0; $P = 0.494$ and 0.596 for the formalin group and 0.077 and 0.039 for the Bouin's group, Table 5). Although the height of midgut cells is stable within each diet and 1 mm interval size category (Table 3), we weighted the midgut cell height by fish size for this analysis because it included both fed and starved larvae ranging between 2.8 and 5.6 mm. When the midgut height of fish belonging to all diets was plotted over the 2.8–5.6 mm size range, midgut cell height increased linearly with size (Fig. 4). And, because the fish shrink in the collecting net and the amount of shrinkage is related to the time elapsed in the net, we adjusted fish lengths in this analysis to equal "capture" size using the model developed by Theilacker (1980).

Applying the Calibration Criteria

In practice, when applying this analysis to the field to estimate starvation-induced mortality rates (Owen et al. 1989), it was deemed necessary to use only three diet categories (fed, intermediate, and starved) instead of the four distinct categories determined by ANOVA (Table 4), and discussed earlier. Because the durations were 5 days for both diets where feeding was delayed 1 and 2 days (S1/F and S2/F), there was no need for the S1/F larvae to be a separate, fourth category. Thus we included S1/F in the intermediate category and selected 5 days as an average duration for the <4.00 mm larvae in this category.

The cell-height intervals for the three categories were the midpoints between the means of the group cell heights determined for the laboratory-reared larvae. We regarded all larvae with a midgut height measurement >17.5 μm as belonging to the fed category; the break between the intermediate and starving categories was 11.25 μm. This classification scheme correctly identified 95% of the fed larvae, 77% of the starved larvae, and 74% of the intermediate larvae <4.00 mm SL.

To calculate the starvation rates of northern anchovy larvae in the sea, we measured the length of each field-collected larva (corrected for

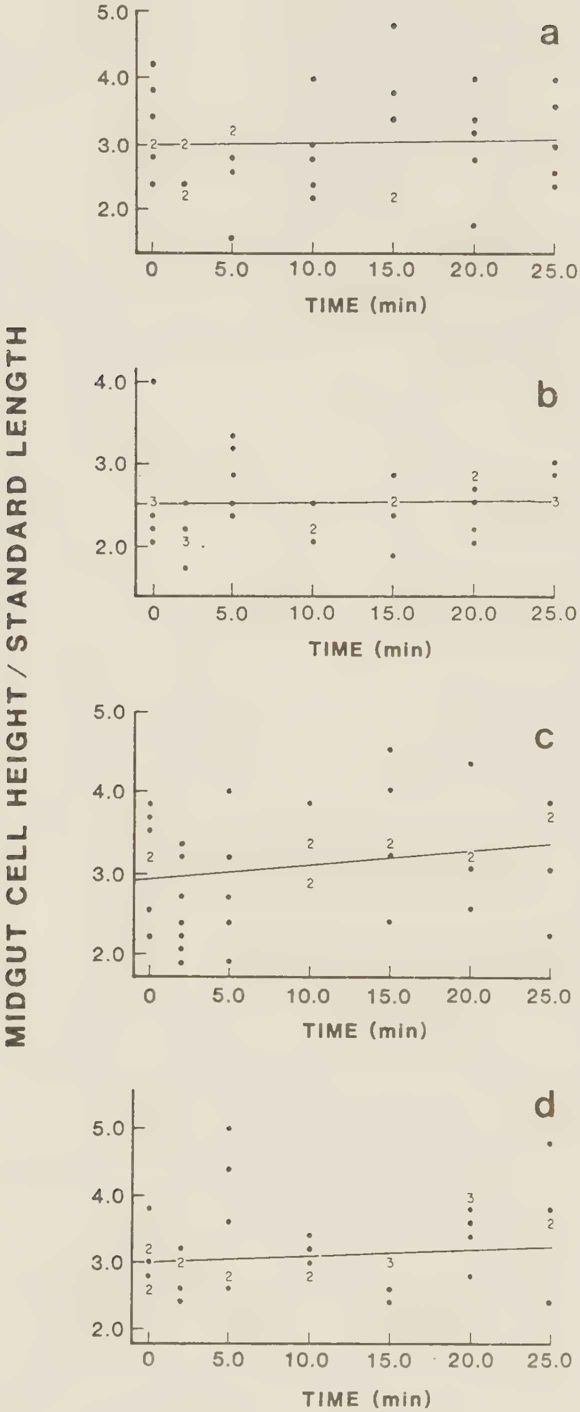

FIGURE 6.—a) Change in midgut cell height measurement over time for formalin-fixed *Engraulis mordax* larvae that were fed. b) Change in midgut cell height measurement over time for formalin-fixed *Engraulis mordax* larvae that were starved. c) Change in midgut cell height measurement over time for Bouin's-fixed *Engraulis mordax* larvae that were fed. d) Change in midgut cell height measurement over time for Bouin's-fixed *Engraulis mordax* larvae that were starved.

shrinkage due to time-in-net and preservation (Theilacker 1980)) and the height of the midgut cells. The adjusted SL and absolute midgut cell height classifies each larva into a size, diet, and midgut cell height category. The numbers of larvae belonging to each category are divided by the category durations to yield the number of larvae per day per category. To estimate the percentage of larvae dying per day due to starvation, the starved category is divided by the total number. An example of these manipulations in Table 5 (taken from Owen 1989; this issue) shows that mortality due to starvation was estimated to be 24%/d for first-feeding anchovy larvae collected off southern California.

Table 5.—Histological condition of larval northern anchovy off southern California. (From Owen et al. 1989: table 7.)

		INSHORE SITE I				
		Categories				
SL mm		Fed "healthy"	Intermediate	Starved	Total	%/d
<4.00	Number[1]	28	17	9		
	Duration[2]	2.5	5	2		
	No./d[3]	11.2	3.4	4.5	19.1	24

[1] Number of field-collected larvae belonging to each size, diet, and midgut-cell-height category.

[2] Response times for each size, diet, and midgut-cell-height category (see text).

[3] Number/duration = No./d.

To complete these manipulations for the next size class, 4–<5 mm, fed and intermediate larvae were discriminated using the same cell height measurement, 17.5 μm, and starved larvae did not grow into this size class (Table 3). The duration for the fed category was 2.5 days and for the intermediate category averaged 3 days. The 2.5 d duration for the fed category was obtained by dividing the size-class interval by the growth rate, 0.41 mm/d. Larvae from the delayed-feeding treatments that belonged to the intermediate category outgrew this size class within 2–4 days (Table 1). Some larvae belonging to the group where feeding was delayed 1 day (S1/F) had recovered and entered the fed category by the time they grew to 4.00 mm.

Cell heights cannot be measured for northern anchovy larger than 6 mm SL as the midgut folds, increasing the absorptive area and making cell heights difficult to measure.

DISCUSSION

The height of northern anchovy midgut cells (taken on sagittal sections that were prepared for histological examination) defines past feeding history. Kostomarova (1962) also measured the height of intestinal cells of larval fishes to evaluate their state of health. Although she found a relation between fish condition and size of midgut cells, the relation was not quantified. In our study, we establish criteria for discriminating the condition of laboratory-raised larvae using the midgut cell height and for estimating rates of starvation in the field.

To validate this technique, it was necessary to measure the effects on the midgut cells of the prolonged processing periods, commonly encountered at sea. The elapsed time for standard ichthyoplankton net hauls to 225 m is 21 minutes, and additional time is needed for washing down the net and for sample preservation (Smith and Richardson 1977). To quantify the effect of collecting time and processing time on autolysis, we simulated the net collection and used a matrix of 8 time periods, ranging from 0 to 25 minutes, followed by preservation in either of two fixatives, Bouin's or formalin. Initially, alcohol also was tested because we anticipated using the same fish to study both growth and condition. (80% alcohol is routinely used to preserve otoliths.) Unfortunately, we found alcohol useless for histopathology.

The height of the midgut cells did not change over the 25 m net treatment, but the standard length decreased. Thus, for field collections, it is not necessary to adjust midgut height for time-in-net, but it is important to correct standard length of field-collected larvae for shrinkage in order to allocate the larvae into the correct length categories. The model (Theilacker 1980) used to adjust length was generated for formalin-preserved anchovy. Perhaps the slight increase noted in the midgut index (midgut cell height/SL) of the Bouin's-fixed specimens (Fig. 6c, d) indicates that the model is overcorrecting for Bouin's. That is, the additional shrinkage caused by fixation (shrinkage in addition to that due to abrasion by the collecting net) is less when Bouin's is used for the final fixative than when formalin is used. This logic, however, is hard to reconcile because Bouin's, made with 20% formalin, is stronger than the 5% formalin solution we used.

Starved fish may be shrinking more during the net treatment than their fed counterparts, further complicating the interpretation of the shrinkage adjustment. But we cannot be certain that this occurred because we did not follow individual larvae during the net treatment. Yet there was a significant decrease in length of starved larvae when the adjusted lengths (corrected to "live length") were regressed and plotted over time (Fig. 7b; Table 6). The decrease in length was not evident for the fed larvae (Fig. 7a). This apparent difference in shrinkage rates between fed and starved larvae needs to be tested.

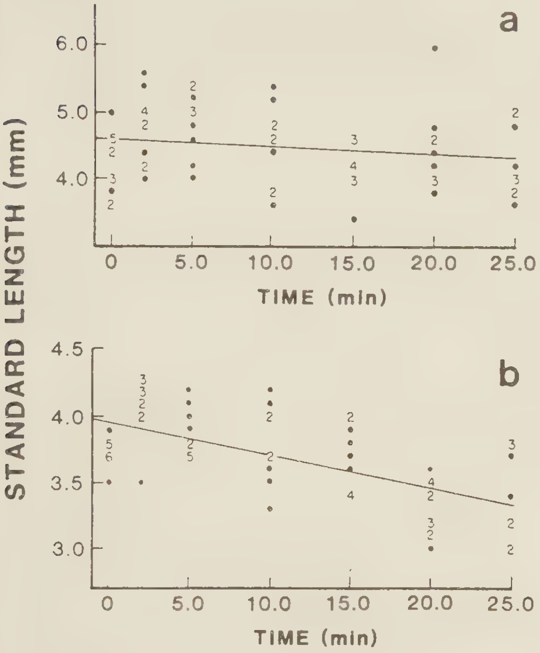

FIGURE 7.—a) Change in standard length over time for fed *Engraulis mordax* larvae that were fixed in formalin and Bouin's. b) Change in standard length over time for starved *Engraulis mordax* larvae that were fixed in formalin and Bouin's.

TABLE 6.—Coefficients for regressions of midgut indexes (midgut cell height/adjusted standard length (mght/SL)) and of adjusted standard length (SL) with elapsed time-in-net (*t*).

			Mght/SL = a + b*t*			
Diet	Measurement	Fixative	a	b	*P*	Reference figure
Fed	Mght/SL	5% formalin	2.8941	0.0092	0.494	6a
Starved	Mght/SL	5% formalin	2.4869	0.0041	0.596	6b
Fed	Mght/SL	Bouin's	2.8961	0.0212	0.077	6c
Starved	Mght/SL	Bouin's	2.9839	0.0231	0.039	6d
Fed	SL	Formalin & Bouin's	3.9605	−0.0251	0.000	7a
Starved	SL	Formalin & Bouin's	4.5813	−0.0124	0.079	7b

Incidental information from delayed feeding experiments (Table 1) revealed that, depending on diet, age of 5 mm northern anchovy ranged between 9 and 19 days. This 10 d range in age at size (due to feeding history) has important implications for size-at-age mortality estimates.

In conclusion, our study indicates that the absolute midgut cell height of northern anchovy larvae is a practical criterion to use for estimating rates of starvation. The cell height measurement yields reliable estimates of feeding history, is resistant to autolysis, and is reliable in formalin-fixed specimens. Thus, the special ichthyoplankton tows and preservatives required for a histopathological index are not needed when the midgut index is used. The midgut index is as sensitive to nutritional conditions as the histological index and does not require the rigorous calibration needed for the morphometric technique (Theilacker 1986; Setzler-Hamilton et al. 1987). Also the midgut character is much easier and faster to measure than scoring the histological features of northern anchovy tissues, and it does not require a solid background in histology for the person scoring. Because of these features, the midgut index is practical for routine estimates of starvation rates of larvae in the sea. In addition, unlike previous methods, the duration of tow is not a constraint because the character does not degrade with time and a sample representative of the water column can be taken.

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8975

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XANTHIC, GIGANTIC, CHINA ROCKFISH

On 18 May 1988 approximately two miles southeast of Crescent City, California (lat 41°42′ N, long 124°10′ W) commercial hook-and-line fisherman Ernie Gentry of the LADY MAE, fishing in 14 fathoms of water with a non-baited barbless hook, caught a 453 mm total length China rockfish, *Sebastes nebulosus*. The fish was shipped to F. Alioto Fish Company in San Francisco and the general manager, Joseph Cincotta, called the author to have the fish identified. This specimen is the largest China rockfish yet captured (Miller and Lea 1972) and the first known to exhibit xanthism.

Xanthism is the property of the skin to be marked by a predominance of yellow pigment. Xanthic fish have been reported on the West Coast for the following species: Dover sole, *Microstomus pacificus* (McCormick and Baldwin 1952); sablefish, *Anoplopoma fimbria* (Phillips 1952); and bocaccio, *Sebastes paucispinis* (Davenport 1966).

Normally China rockfish are a mottled brown or blue-black mixed with yellow and have a yellow stripe running from the anterior spines (between spines III and IV) of the dorsal fin down to the lateral line and thence along the lateral line to the caudal peduncle (Ayres 1854, Miller and Lea 1972). This specimen was a bright golden yellow with a few tiny black spots on the head and several small patches of black on the dorsal fin membrane between the second and seventh dorsal spines (Figure 1)

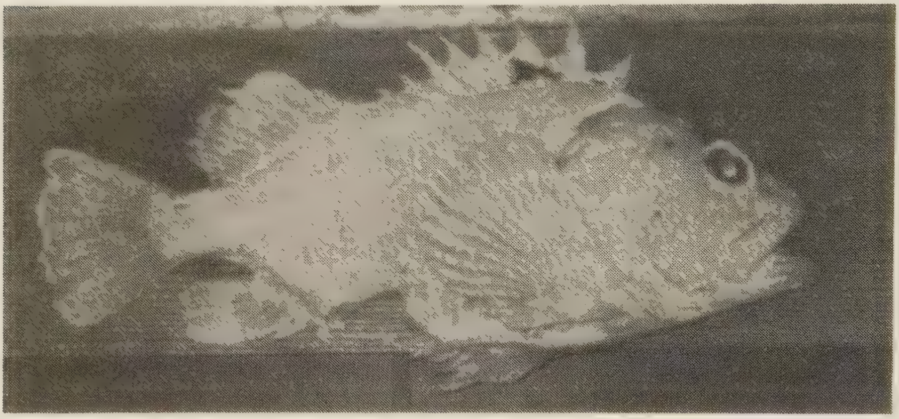

FIGURE 1. Xanthic, gigantic, China rockfish caught off Crescent City, California.

All the China rockfish's physical attributes correspond to those described for this species (Ayres 1854, Phillips 1952, Miller and Lea 1972). The total length of 453 mm exceeds the previously reported total length of 432 mm by five percent. This specimen had seven anal fin rays, 10 unbranched and 18 total pectoral fin rays, 13 dorsal fin rays, and 29 gill rakers ($8 + 21 = 29$). The following measurements were taken: standard length (367 mm), head length (148.6 mm), orbit width (32.2 mm), bony interorbital width (19.8 mm), suborbital height (14.1 mm) and pectoral length (109.7 mm).

The age of this fish was determined by four scientists experienced in aging rockfish using the experimental broken and burnt otolith method (Chilton and Beamish 1982). All scientists agreed that the fish was approximately 70 years old (ca. 1918 year class).

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8976

Trends in the Fisheries for Billfishes in the Pacific

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The status of commercial fisheries for billfishes prior to 1970 was reviewed at the 1972 International Billfish Symposium (Ueyanagi 1974) and can be summarized: (1) Billfishes are taken primarily by the tuna longline fishery; (2) most are captured incidentally;(3) although billfish catches may be incidental to the tunas, they are nevertheless regarded highly in Japan with some species commanding high prices in the markets as *sashimi* (sliced raw fish usually eaten with soy sauce and horseradish); (4) Japan's tuna longline fishery covered virtually the entire distributional range of the billfishes by 1965, about the same time its billfish production peaked; and (5) during the 1960s, the catches of various billfish species were high but, around 1963, blue marlin *(Makaira mazara)* catches began declining in the South Pacific region, while catches of striped marlin *(Tetrapturus audax)* tended to fluctuate markedly from year to year.

During the 16 years since the 1972 International Billfish Symposium, certain characteristics of the billfish fisheries and resources have remained virtually unchanged while others have undergone marked changes. For example, the characteristics listed in (1), (2), and (3), above, are essentially the same today as in the pre-1970 period. There have been changes in the target species, fishing areas, fishing seasons, and fishing methods (e.g., fishing at greater depths) over the past several decades by distant-water fishing nations that have undoubtedly affected the catch and species composition in the longline fishery. Thus, interpretation of the billfish resources based on nominal catch-and-effort data must be viewed cautiously. The present discussion will focus on the post-1970 years, although some references will be made to the pre-1970 period.

Utilization and Markets

Billfishes are utilized in Japan as *sashimi*, as an ingredient for *sushi*, or sold as *kirimi* (fillet) to be broiled or baked. They are also processed into *kasuzuke* (fish preserved in *sake* lees) or *misozuke* (fish preserved in *miso*, a soybean paste). In the past, billfishes have been used as ingredients in manufacturing sausage and ham.

In other countries, the demand for billfishes is increasing as a food product, especially for swordfish, which is highly prized in the U.S.A. markets as "steaks." The billfish catches of the Korean and Taiwanese longline fleets based in American Samoa are reported to be directed at the Japanese markets (G. Yamasaki pers. commun.). Finally, a major effort has been made in recent years by recreational fishing interests in the Pacific to have fishermen tag and release their billfish catches in order to obtain information on migration pathways and to maintain viable billfish populations.

At the Tokyo Fish Market, the average prices of billfishes increased markedly during the 1970s, with the exception of sailfish *(Istiophorus platypterus)* and shortbill spearfish *(Tetrapturus angustirostris)*; Fig. 1 (Tokyo Metropolis 1987). The price increase for striped marlin was especially pronounced — nearly threefold from 1970 to 1985. The sharp increase in market prices after 1967 was due to certain technological developments in the Japanese tuna longline fishery. In a quest for southern bluefin

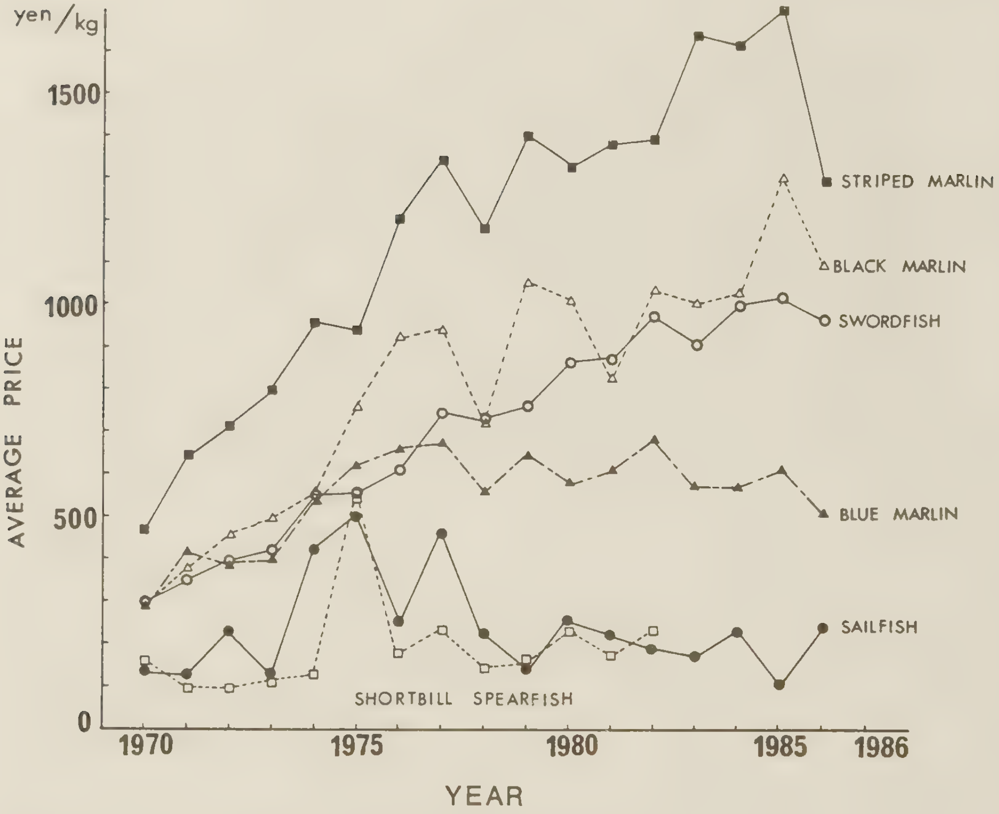

Figure 1. Average prices of billfishes (fresh) at the Tokyo Fish Market, 1970-1986.

tuna *(Thunnus maccoyii)*, the Japanese longline began outfitting their vessels with freezers capable of quick-freezing fish to ‹-55°C. The frozen fish were then maintained in fishholds at ‹-40°C. Billfishes brought back to Japan under such refrigerated conditions were in great demand in the *sashimi* market; this was especially true for striped marlin. The rate of increase in prices slowed around 1977; prices remained relatively stable in the early 1980s.

Review of the Fisheries

Trends in Catch

Based on total landings, catches of striped marlin were low [7,000 to 9,000 metric tons (mt)] in 1955-1960, high (ca. 23,000 mt) in 1964-1971, and then relatively low (10,000 to 15,000 mt) in 1972-1985 (Fig. 2A). A more detailed examination of the available data is required to determine whether the post-1972 decline in striped marlin catches reflects a true reduction in abundance or results from a change in fishing strategy (e.g., use of deeper fishing longline gear).

Catches of black marlin, *Makaira indica* (Fig. 2A), and blue marlin (Fig. 2B) declined as well. Black marlin catches were 5,000 to 6,000 mt annually from 1955 to 1958, then slowly declined to around 3,000 mt in 1985. Except for a notable peak in 1961-1963, blue marlin catches fluctuated between 12,000 and 19,000 mt since 1964.

The combined annual catch of sailfish and shortbill spearfish was 3,000 mt in the 1950s (Fig. 2B). The catch increased to nearly 13,000 mt in 1965, remained at that level until 1969, then steadily declined to 3,100 mt in 1985. The 1976-1978 catch of sailfish and spearfish is not included in Figure 2B because the data are questionable.

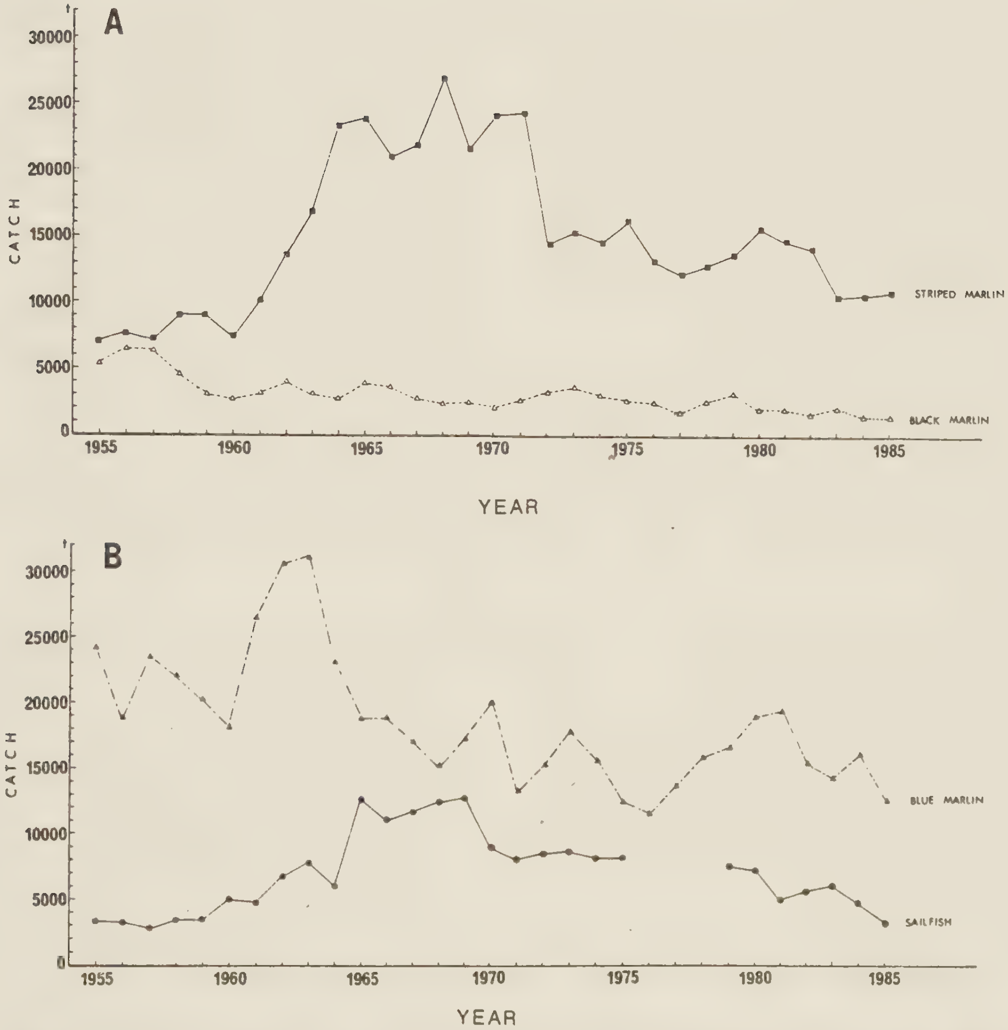

Figure 2. Annual catch of billfishes in the Pacific Ocean, 1955-1985: (A) striped marlin and black marlin;(B) blue marlin and combined catches of sailfish and shortbill spearfish. Data are from Shomura (1980) and the FAO (1976, 1979, 1984, 1987).

Trends in the Longline Fishery

The commercial catch of billfishes by the longline fishery, which primarily targets various tuna species, increased as the fishing grounds expanded. Since the 1960s, most of the catch has been made by the longline fishery. The expansion of the longline fishery has been described by Ueyanagi (op. cit.). The Japanese longline fishery in the Pacific gradually began expanding eastward in the early 1950s. By 1965, the fishery had extended throughout the tropical and subtropical waters of the Pacific and, thus, covered virtually the entire distributional range of the various billfish species. The habitats of the billfishes caught by longline ranged from temperate to tropical waters and from coastal to offshore waters. During the late 1960s and early 1970s, the Japanese longline fleet began focusing on the southern bluefin tuna and bigeye tuna *(Thunnus obesus);* thus, the Japanese fleet's effort in the subtropical zones was reduced. The longline fleets of Korea and Taiwan, however, filled that void in the South Pacific (Ito and Yamasaki in press).

Japan's Longline Fishery

During the 1970s, the Japanese longline fishery made a substantive change in its fishing operation. The gear for many fishing vessels was modified to fish in deeper waters for bigeye tuna. Around 1970, bigeye tuna constituted about 30% of the tuna and billfish catches and, by 1980, had increased to 40%. This increase has been attributed to the deeper fishing longline gear. The shift to a deeper fishing mode has undoubtedly changed the catchability coefficient for several species, including the billfishes, taken by longline gear. In 1970, the billfish catch comprised about 21% of the total longline catch; by 1980, the billfish percentage had declined to 13%. Because billfishes are generally considered to inhabit the upper strata of the water column, the change in longline gear may have resulted in a major change in catch per unit of effort (CPUE).

Changes in Longline Fishing Grounds

During the late 1960s and early 1970s, Japanese longline fishing effort was concentrated in the high latitudes of the Southern Hemisphere near Australia and New Zealand for southern bluefin tuna, in the temperate and tropical waters of the central and western Pacific for yellowfin tuna *(Thunnus albacares)* and bigeye tuna, and in the waters off Mexico for striped marlin (Fig. 3). By 1975, fishing effort in the coastal waters of Mexico had decreased substantially (Fig. 3). Longline fishing effort increased markedly in the equatorial region of the central and eastern Pacific in the 1980s (Fig. 3), principally because of the success in catching the highly prized bigeye tuna in deeper waters. According to Suzuki (in pres), longlining comprised more than 50% of all fishing operations in the equatorial waters in 1980. Since deep longlining is less effective in catching billfishes than is conventional

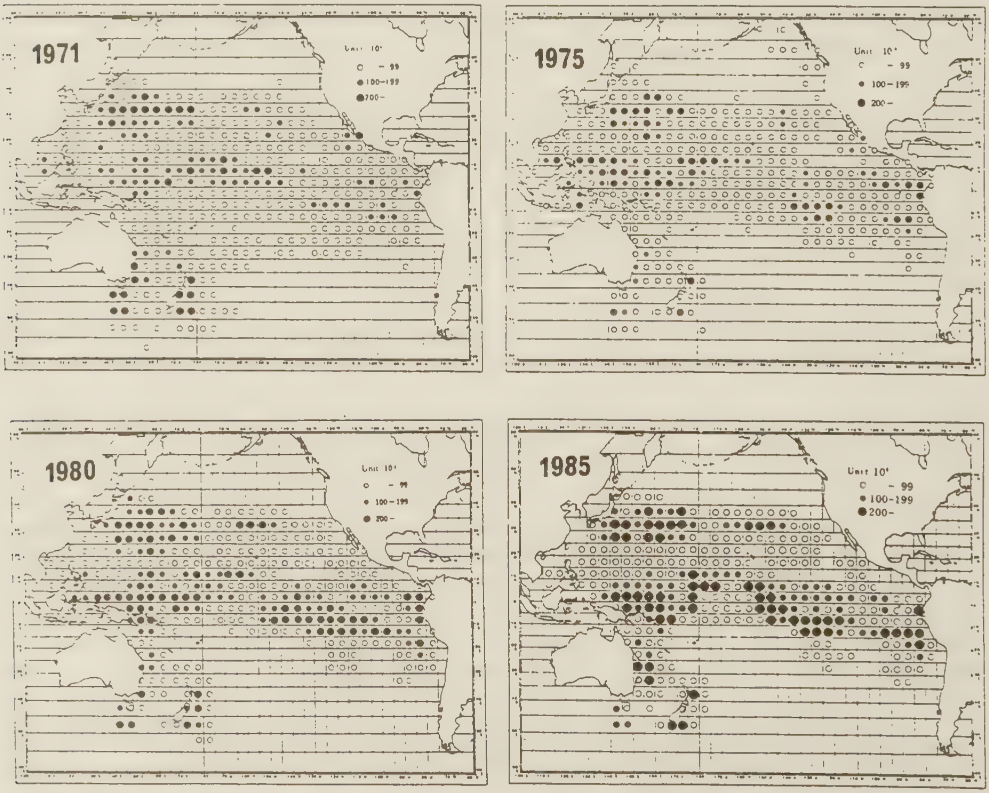

Figure 3. Comparisons of the distribution of estimated total fishing effort (in number of hooks) expended by the Japanese tuna longline fishery for 1971, 1975, 1980, and 1985 (from the Fisheries Agency of Japan 1973, 1977, 1982, unpub. data).

longline gear (Miyabe and Bayliff 1987), the production of billfishes obviously has been affected by the increased use of deep longline gear. The equatorial region later experienced further increases in the use of deep longline gear, which constituted about 90% of all longline operations in the area in 1985 (Suzuki in press).

Catch and Effort

The total fishing effort (in number of hooks) expended by the Japanese longline vessels in the Pacific Ocean apparently leveled off at around 280 million hooks per year during the first half of the 1970s (Fig. 4). A trend toward increased effort occurred, however, during the second half of the 1970s. After peaking in 1981 at around 400 million hooks, fishing effort declined and leveled off at around 330 million hooks after 1983. The increase in total fishing effort during the second half of the 1970s reflects the increase in the number of hooks fished per longline operation. On the other hand, the decrease in fishing effort in 1982 and 1983 is believed attributable to the 20% *gensen* (fleet reduction) in the tuna longline fishery during 1981-1982.

Because the longline fishery is responsible for a large share of the billfish catches in the Pacific, the trends in longline catch of billfishes (Fig. 4) are generally similar to those discussed earlier under the total billfish catch.

CPUE by Area

The annual variations in CPUE (number of fish caught per 1,000 hooks fished) of the principal billfish species were examined for three areas in the Pacific: Area 1, north of lat. 15°N; Area 2, lat. 15°N-15°S; and Area 3, lat. 15°-30°S (Fig. 5). Because the fishing effort (in number

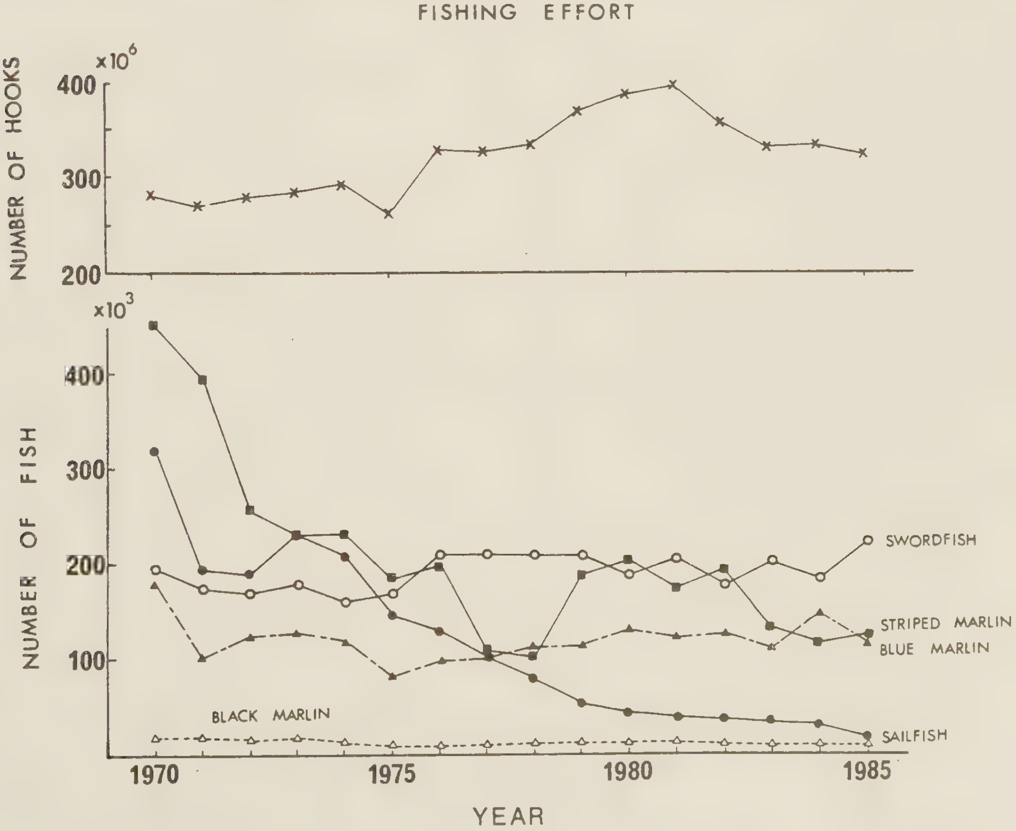

Figure 4. Annual fishing effort (in number of hooks) and catch of billfishes by the Japanese tuna longline fishery in the Pacific Ocean, 1970-1985.

of hooks) used to obtain CPUE is nominal, unstandardized effort, the CPUE values are not intended to reflect accurately the absolute resource levels, and interpretations based on these statistics should be viewed with caution.

In Area 1, fishing effort initially decreased during 1970 to 1975, thereafter stabilizing at 80 to 100 million hooks (Fig. 5). The CPUE for striped marlin decreased markedly and, by 1975, was only one-half that in 1970; thereafter, the CPUE fluctuated between 0.5 and 1.0 fish per 1,000 hooks. Swordfish CPUE was generally stable at around 1.0 fish per 1,000 hooks. In Area 2, fishing effort increased steadily from

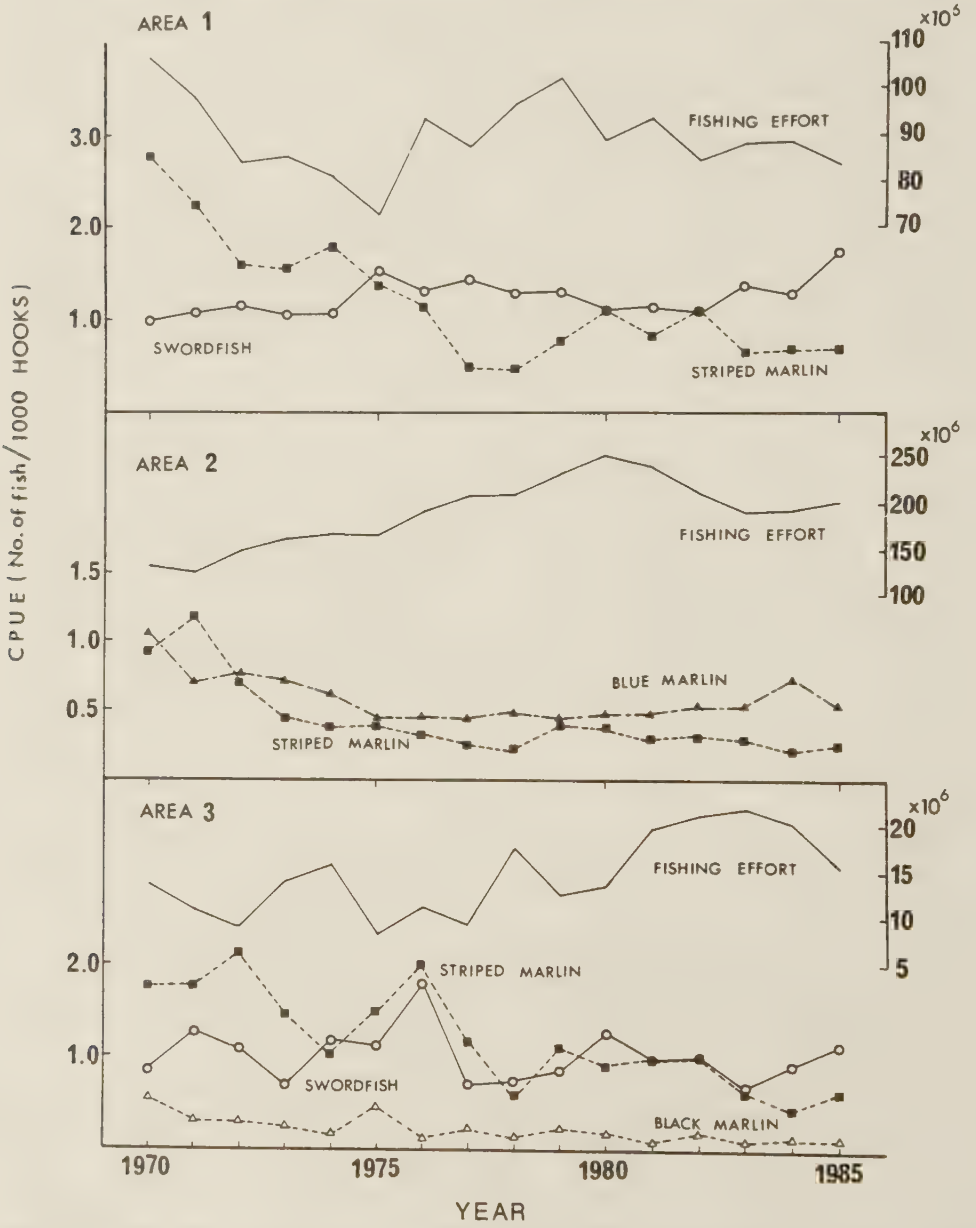

Figure 5. Annual fishing effort and catch per unit effort for principal billfish species by area, 1970-1985: Area 1, north of lat. 15°N; Area 2, lat. 15°N-15°S; and Area 3, lat. 15°-30°S.

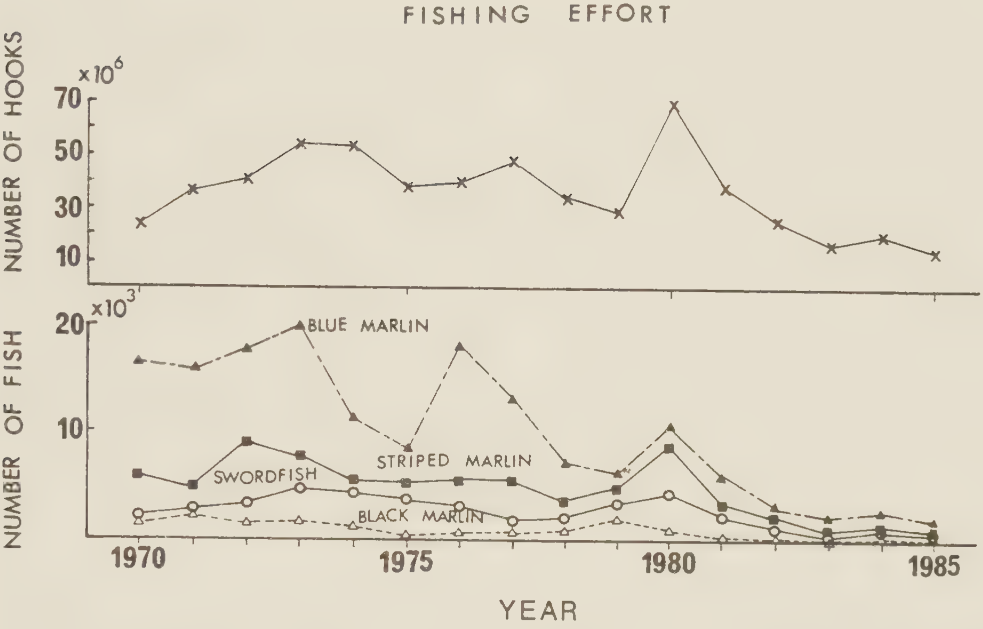

Figure 6. Annual fishing effort (in number of hooks) and catch of billfishes, by species, by the Taiwanese tuna longline fishery in the Pacific Ocean, 1970-1985.

1970 to 1980, reaching a peak of 250 million hooks in 1980 (Fig. 5). Effort declined subsequently, then stabilized at about 200 million hooks. The catch rate for blue marlin, the principal billfish species taken in this region, declined during the first half of the 1970s and, since then, has been stable at about 0.5 fish per 1,000 hooks. The striped marlin CPUE decreased steadily during the first half of the 1970s and stabilized thereafter at about 0.3 fish per 1,000 hooks.

Of the three areas, Area 3, the southernmost sector, had the lowest level of fishing effort (Fig. 5). Fishing effort was 10 to 15 milion hooks during most of the 1970s, reached a high of about 22 million hooks in 1983, then dropped to 15 million hooks in 1985. The striped marlin CPUE fluctuated dramatically; however, apparently the average CPUE for the first half of the 1980s was lower than in the 1970s. Some fluctuations occurred in swordfish CPUE, but there were no long-term upward or downward trends. Black marlin CPUE declined slightly from 1970 to 1985.

Taiwan's Longline Fishery

The Taiwanese distant-water longline fleet generally concentrates its fishing effort in the southerly latitudes of the central and western Pacific; albacore *(Thunnus alalunga)* is the tuna species sought by the fleet (Wetherall and Yong 1984). Fishing effort (in number of hooks) and catch (in number of fish) by species, based on available catch statistics (Tuna Research Center 1979, 1986) are presented in Figure 6. The total Taiwanese fishing effort in the Pacific fluctuated between 30 and 55 million hooks in the 1970s. Except for a peak of 70 million hooks fished in 1980, effort in the 1980s thus far has been around 20 million hooks. A general decline in blue marlin catch appears to have occurred over the 1970-1985 period, although some fluctuations are apparent. The striped marlin catch fluctuated between 5,000 and 9,000 fish from 1972 to 1980, then declined steadily from 1980 to 1985, probably reflecting the decline in fishing effort during the same period. In general, the swordfish *(Xiphias gladius)* and black marlin catches also declined over this 1970-1985 period.

In addition to the distant-water longline fleet, a fleet of smaller longline vessels operates exclusively in the coastal waters of Taiwan. The average annual catch by species for the 1975-

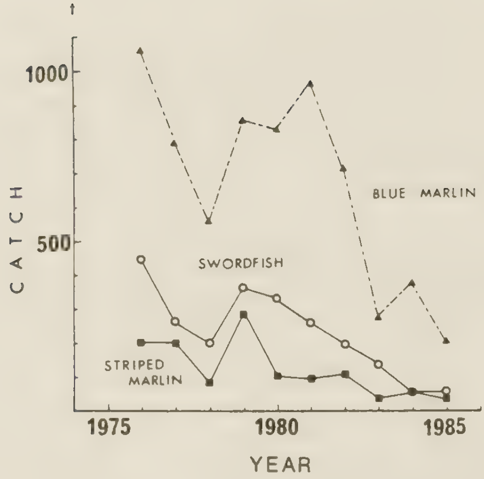

Figure 7. Annual catch of billfishes by the Korean tuna longline fishery, 1975-1985.

1986 period for the coastal fleet was 750 mt for striped marlin, 1,700 mt for blue marlin, 900 mt for black marlin, and 1,300 mt for sailfish (G. Sakagawa pers. comun.).

Korea's Longline Fishery

In general, the Korean longline fleet has operated throughout the tropical and subtropical Pacific. Effort was generally directed toward the yellowfin and bigeye tunas; thus, the Korean fleet tended to operate in more tropical waters than the Taiwanese longline fleet. Based on available statistics (Fisheries Research and Development Agency 1980, 1981, 1985), total fishing effort (in number of hooks) expended by the Korean longline fleet in the Pacific fluctuated between 60 million and 100 million hooks from 1975 to 1980. The annual catch of billfishes, by weight and by species, for 1976-1980, based on FAO (1979, 1984, 1987) statistics, is shown in Figure 7. The blue marlin catch declined markedly: from >1,000 mt in 1976 to about 200 mt in 1985. Striped marlin and swordfish catches also declined from 1976 to 1985.

Other Longline Fishing Effort

In addition to the large longline fleets of Japan, Korea, and Taiwan, other longline operations include a small fishery based in Hawaii, one longliner based in American Samoa, one longliner in Tonga, and a fleet in Indonesia. Hawaii's longline fleet has declined in numbers since the 1950s, from a high of 76 vessels in operation in 1950 to 22 vessels in 1980. The vessels are small, generally 9 to 12 m long. New vessels have joined the longline fleet in recent years, and active longliners numbered 37 in 1984. The increase in fishing activity is due to increased fish prices and the expanded market, which includes airfreighting fresh tunas and billfishes to Japan and the continental U.S.A. to meet the increased demand for *sashimi*-quality fish. The total catch of the Hawaiian longline fishery equaled 1,695 mt in 1987 (Pooley 1988), of which the billfishes comprised 22.1%. Striped marlin and blue marlin constituted about 68.9% and 12.5%, respectively, of the total billfish catch. Small amounts of swordfish, black marlin, shortbill spearfish, and sailfish were also landed by the longline fleet.

Other Fisheries for Billfishes

Gill-Net Fishery

A gill-net fishery for billfishes and tunas has been operational in Japan for over 100 years. During the early years, fishing was confined to coastal waters. Since the 1970s, however, the fishery has expanded offshore as a result of the development of the ome ami (drift gill-net) gear and a shift in target species. The principal fishing areas of the ome ami fishery during the first half of the 1970s were the waters off the Sanriku district of Honshu Island, off Boso Peninsula, the South China Sea, and the Yellow Sea. In the ome ami gill-net fishery, a standard operation uses 12 km of net (17 to 18 cm mesh size). Using netting of >12 km per operation and mesh sizes of <15 cm by Japanese flag vessels is prohibited by regulations imposed by the government. Fishing vessels are 50 to 500 gross tons (usually, 90 to 100 gross tons). The vessels are used in other fisheries (e.g., salmon drift gill net, squid gill net, saury stick-held dip net, tuna longline, and squid jigging.

The gill-net fishery's catches of billfishes, tunas, and other species from 1970 to 1986 are listed in Table 1. The total billfish catch from 1973 to 1986 fluctuated between 3,600 and 10,200 mt. Some fluctuations have been attributed to changes in target species and in the number of vessels operating in the fishery. During the early 1970s, billfishes were the target species by the gill-net fishery; however, since the early 1980s, there has been a shift to target the tunas, especially albacore. Thus, the decline in the billfish catch may reflect the shift in target species rather than a decline in the billfish population. Striped marlin comprised more than 50% of the total billfish catch: swordfish was about 25%. The blue marlin catch. which includes black marlin. has declined in recent years.

The distribution of striped marlin catches in the ome ami gill-net fishery for 1985 is based on catches by vessels over 10 gross tons (Fig. 8). The main fishing grounds for striped marlin are in the western Pacific. The catch sizes were 15 to 90 kg for striped marlin and 5 to 170 kg for swordfish (weights are based on the total weight less the weight of snout and viscera).

A commercial drift gill-net fishery in California. started in 1980. was directed at swordfish. discussed fully by Sakagawa (this volume). It is noted, here. only that small numbers of striped marlin are taken in this fishery: more than 90% of the billfish catch is swordfish.

Harpoon Fishery

Harpoon fisheries directed at billfishes are operated in coastal waters of Japan. Taiwan. and California. The annual billfish catch by the Japanese harpoon fishery. 1959-1971, fluctuated between 2.200 and 4.600 mt. It declined markedly after 1972, then has been stable at a level of less than 1,200 mt (Fig. 9). The average catch over the last 10 years was around 800 mt. Striped marlin are the main target of this fishery. making up about 50% of the total billfish catch. Swordfish and blue marlin (including black marlin) are next in importance. each representing around 20% of the total catch. The fishing grounds are located in waters around Izu and Bonin Islands and off Sanriku district of Honshu Island. The fishing vessels average <20 gross tons: most are 5 to 15 gross tons.

The total monthly catch of billfishes. by species. landed at the port of Shimoda. Japan. 1972-1978. is given in Figure 10 (Matsuoka and Tsuchiya 1979). Striped marlin are landed during January to July: the peak occurs in March. Blue marlin are landed in April and December: the high catches are in September and October. Swordfish are landed over an extended period: the peak occurs in May. Black marlin are landed in May-October: the peak period is in July-August. The body weights (viscera removed) of billfishes landed by the harpoon fishery are 20 to 70 kg (mean, 55 kg) for striped marlin. 90 to 260 kg (mean, 135 kg) for blue marlin. 30 to 200 kg (mean, 105 kg) for swordfish. and 60 to 220 kg (mean, 117 kg) for black marlin.

The average annual catch of the Taiwanese harpoon fishery for billfishes. during the period 1975-1986. was 130 mt for striped marlin and around 500 mt each for blue marlin. black marlin. and sailfish (G. Sakagawa pers. commun.).

A commercial harpoon fishery directed toward swordfish has operated in California waters since about 1913. Striped marlin can be taken

Table 1. Catch statistics of the Japanese gill-net fishery[1]. 1970-1986.

Year	Striped marlin	Swordfish	Blue marlin[2]	Sailfish	Subtotal	Tunas	Skipjack tuna and frigate mackerel	Total[3]
1970	3	—	—	126	129	44	169	328.687
1971	10	1	—	54	65	32	146	347.611
1972	243	55	8	55	361	135	626	296.867
1973	3.265	720	268	98	4.351	348	548	311.628
1974	3.112	1.304	230	83	4.729	614	350	325.539
1975	6.534	2.672	795	149	10.150	951	507	295.050
1976	3.561	3.488	580	117	7,746	2.403	920	295.270
1977	4.424	2.344	998	398	8.164	1.599	1.864	322.777
1978	5,593	2.475	884	343	9,295	6.393	2.078	306.326
1979	2.532	983	513	347	4,375	4.464	1.012	301.484
1980	3.467	1.746	868	137	6.218	4.728	1.134	296.929
1981	3.866	1.848	1.165	362	7.241	12,749	2.571	327.649
1982	2,351	1.257	954	333	4.895	14,292	4.314	350.631
1983	1.845	962	931	276	4.014	6.611	3.933	291.950
1984	2.257	971	240	110	3,578	8.045	5,110	362.607
1985	2.323	1.026	401	146	3.896	10.599	2.471	376.129
1986	3.536	1.170	176	233	5.115	8.012	6.344	351.888

[1] including ome ami gill-net. spanish mackerel gill-net. flying fish gill-net, saury gill-net. herring gill-net. etc.

[2] including black marlin

[3] including other fishes (sharks. cods. atka mackerel. flat fishes. spanish mackerel. etc.)

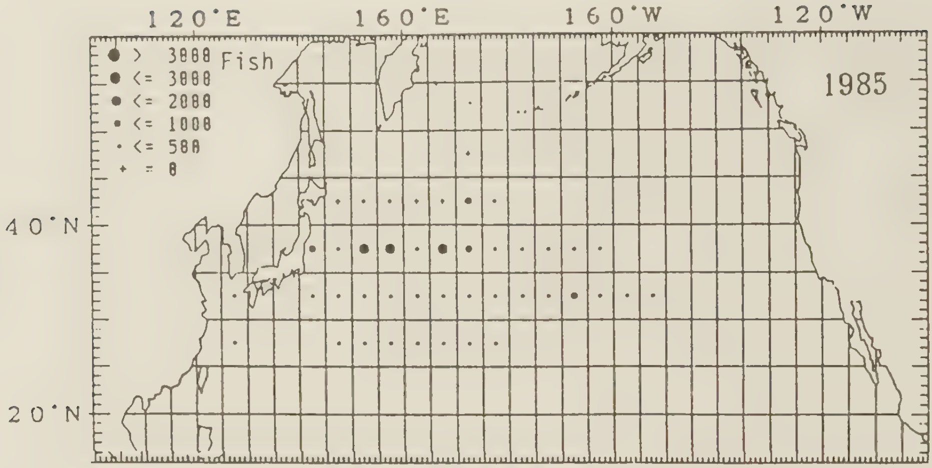

Figure 8. Distribution of striped marlin catch of the Japanese gill-net fishery for 1985.

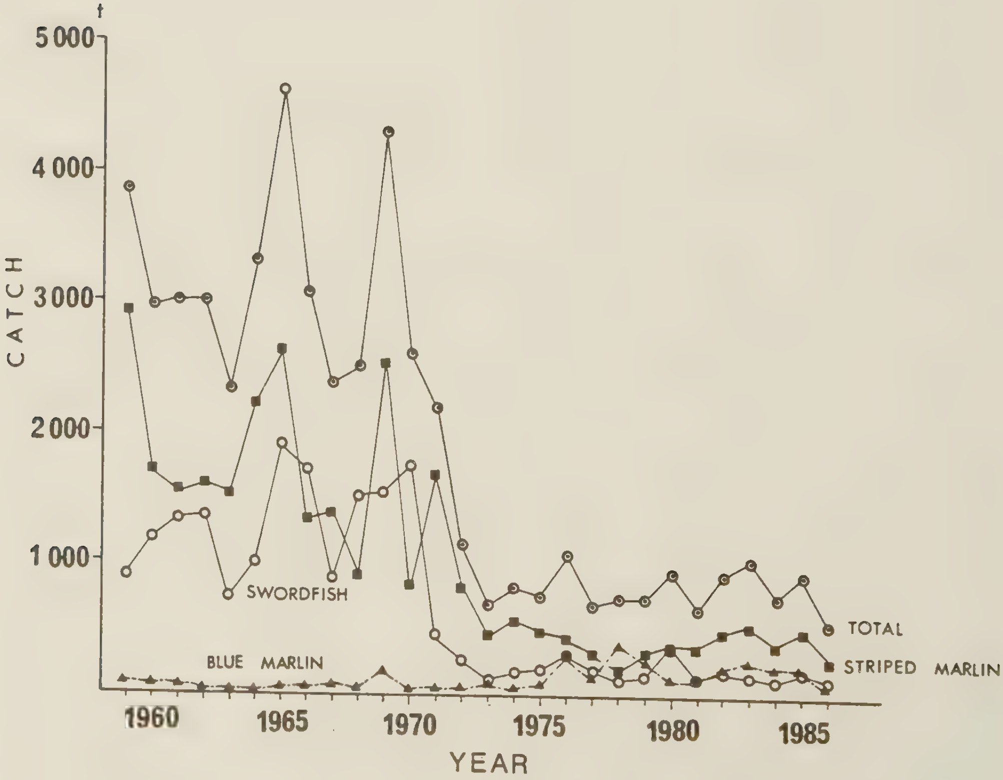

Figure 9. Total annual catch of billfishes landed by the Japanese harpoon fishery, 1959-1985.

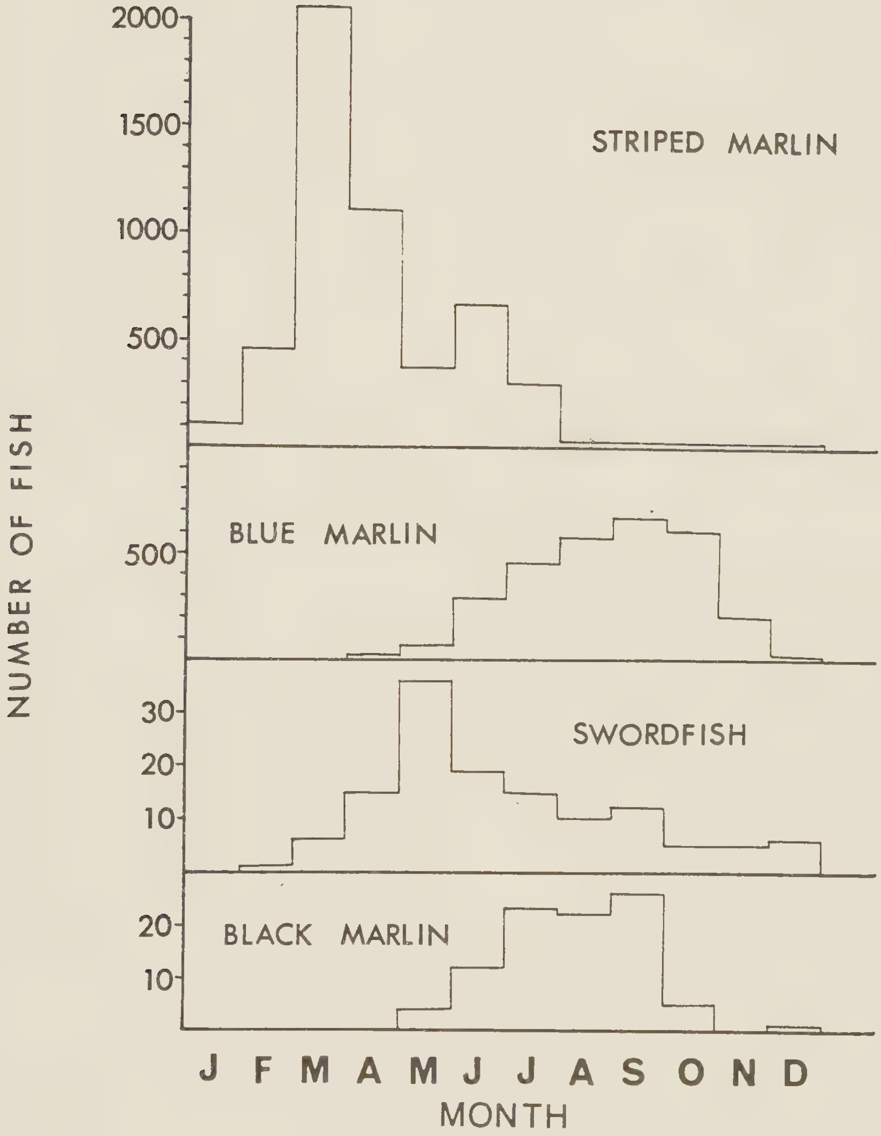

Figure 10. Monthly total catch of billfishes, by species caught by the Japanese harpoon fishery and landed at Shimoda, 1972-1978. Data are from Matsuoka and Tsuchiya (1979).

in this fishery, but the sale of this species is prohibited by the State of California. Thus, there are presently no reported landings of striped marlin (Anonymous 1979).

Purse-Seine Fishery

The incidental catch of billfishes by Japanese single purse-seiners operating in the tropical waters of the western Pacific from 1985 to 1987 is shown in Table 2. The billfishes made up only 0.1% of the total purse-seine catch. Blue marlin were the dominant species caught by the purse-seiners; they represented 99.3% of the total billfish species taken, sailfish and black

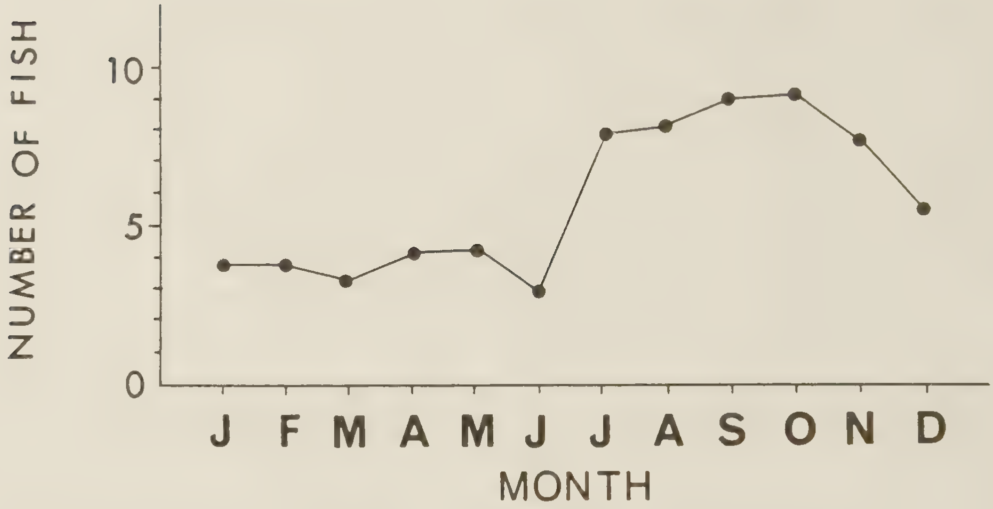

Figure 11. Average monthly catch of billfishes per cruise of the Japanese single purse-seiners in 1987.

marlin representing 0.05 and 0.02%, respectively, of the total billfish catch. No records are available on striped marlin or swordfish taken by Japanese purse-seiners. The average monthly catch of billfishes in 1987 was about four fish per January-June cruise and eight fish per July-December cruise (Fig. 11). The blue marlin caught by the Japanese single purse-seiners were 10 to 250 kg; a dominant mode was noted at 50 to 60 kg.

Set Net Fishery

Billfishes are also caught incidentally by the set-net fishery. The average annual billfish catch by the set-net fishery in Japan, 1970-1986, was about 360 mt (Ministry of Agriculture 1982, 1987). Sailfish was the dominant billfish species in the catch.

Recreational Fishing

Recreational fishing directed at billfishes occurs throughout the Pacific (Goadby 1970). Important sites include the coastal communities along the southerntip of Baja California, the mainland of Mexico, the Hawaiian Islands, the Bay of Plenty in New Zealand, and eastern Australia (de Sylva 1974). Other sites with growing recreational interests include Fiji, French Polynesia, Guam, the Commonwealth of the Northern Mariana Islands, and Coastal communities along Central and South America.

Table 2. Incidental catch of billfishes by Japanese single purse-seiners, 1985-1987.

		1985			1986			1987	
Month	**No. of boats**	**Tons**	**%***	**No. of boats**	**Tons**	**%***	**No. of boats**	**Tons**	**%***
January	18	14.1	0.14	23	11.7	0.10	18	9.1	0.10
February	20	12.9	0.12	19	6.5	0.06	18	10.3	0.11
March	18	12.1	0.13	29	9.1	0.06	22	8.2	0.07
April	21	10.0	0.09	25	11.0	0.08	16	6.7	0.08
May	20	9.9	0.09	18	8.6	0.09	19	9.0	0.08
June	19	8.9	0.08	21	12.9	0.12	20	5.8	0.05
July	19	9.9	0.10	14	11.8	0.16	11	7.8	0.12
August	14	10.2	0.13	18	13.1	0.15	18	15.5	0.15
September	19	15.4	0.15	13	11.3	0.17	11	10.4	0.17
October	10	6.5	0.12	25	19.8	0.15	15	13.8	0.15
November	19	8.3	0.08	19	8.0	0.08	17	9.9	0.09
December	17	12.4	0.14	25	15.4	0.11	17	7.0	0.06
TOTAL	214	130.5	0.11	249	139.2	0.10	202	113.5	0.10

*%: Billfish catch/total catch

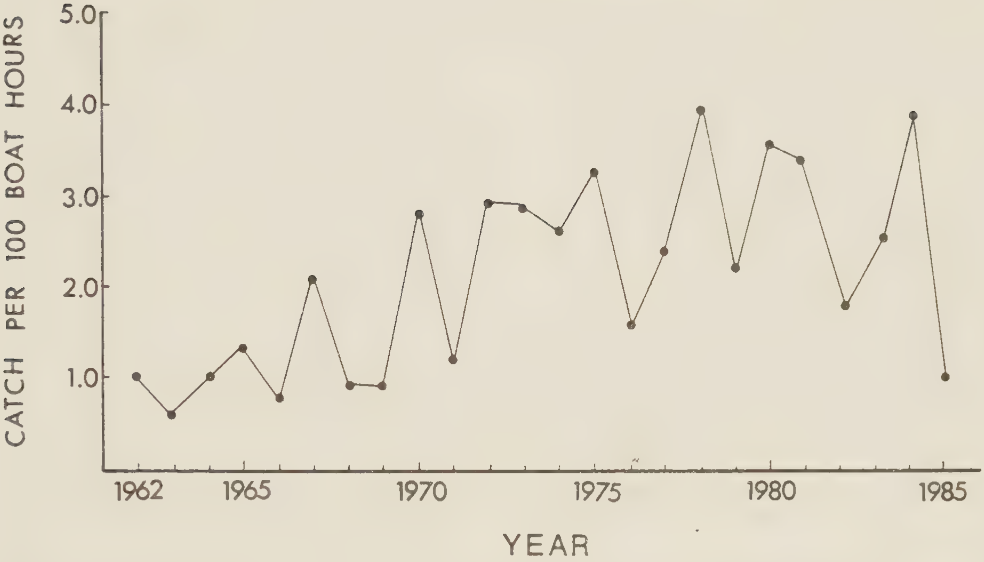

Figure 12. Blue marlin catch per unit effort (per 100 boat-hours) for the Hawaiian International Billfish Tournament, 1962-1985.

Presently, no good estimates are available on the total billfish catch and effort expended by recreational fishing vessels in the Pacific. Although catch-and-effort statistics of commercial fishing activities are generally maintained by government offices, data on recreational fishing activities are sadly lacking in many countries. Some measure of the trends in availability of billfishes is provided by the results of the Pacific Billfish Angler Survey (Squire 1987). Unfortunately, the survey is based on a select population of recreational fishermen, so it does not allow for estimates of Pacific-wide total catch or effort. The 1986 survey reported 13,711 fishing days and a catch of 6,949 billfish for the Pacific (Squire 1988).

The blue marlin CPUE fluctuated markedly from year to year, based on the Hawaiian International Billfish Tournament records from 1962 to 1985 (Fig. 12). An eightfold range in blue marlin CPUE occurred. Although recreational fishing data provide some indication of the status of stocks, caution should be exercised in interpreting those data. Some of the fluctuations are attributable to changes in availability and abundance; however, man-induced changes should not be overlooked. The general trend in recreational fishing is toward use of lighter line and tackle. Because catch-and-effort statistics are usually based on landed catch, the presumed increase in fish loss associated with the lighter tackle is not accounted for in the analysis. A high-priority need exists for a more complete assessment of the catch and effort for billfishes by the entire recreational fishing community in the Pacific. This need probably exists for other oceans, as well.

General Discussion

Billfishes are taken by a wide variety of fishing gear types; however, longline gear has been the principal method of capture over the past several decades. In recent years, the shift in target species of the longline fishery toward bigeye tuna, by using deeper fishing gear, has added a complexity to the use of catch-and-effort statistics as measures of resource abundance. Although Japanese longliners have shifted their fishing effort to high-priced tuna species, they have been replaced in some areas by Taiwanese and Korean longliners.

The gill-net, purse-seine, and recreational fisheries have experienced changes in billfish catches. The catch of billfishes by the Japanese gill-net fishery declined in recent years, principally because of a shift in target species to albacore. A newly developed tuna purse-seine fishery in the western central Pacific has resulted in the capture of small quantities of billfishes by the Japanese single purse-seine vessels. Finally, the billfish catch by a large, widely dispersed recreational fishing community in the Pacific may be increasing; however, details of its magnitude in terms of catch and effort are still lacking.

Acknowledgment

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Shoji Ueyanagi was graduated from Tokyo University in 1950, and received the Dr. (Agr.) degree from Tokyo University in 1961. Since 1950, he has been engaged in tuna and billfish research at the Nankai Regional Fisheries Research Laboratory, Kochi, and at the Far Seas Fisheries Research Laboratory, Shimizu, to 1983. Since then, he has been Professor, Faculty of Marine Science and Technology, Tokai University, at Shimizu, Japan.

Richard S. Shomura received his B.S. and M.S. degrees (zoology) from the University of Hawaii. He was employed for 38 years in various federal fisheries agencies of the United States, most recenlty for several years as director of the Honolulu Laboratory, Southwest Fisheries

Center, National Marine Fisheries Service. He retired from the federal service in September, 1988. Currently, he is a research scientist with the University of Hawaii's School of Ocean and Earth Science and Technology. He also chaired the Second International Conference on Marine Debris, held in April, 1989, at Honolulu.

Yoh Watanabe received the degree of Dr. (Agr.) from Tohoku University in 1973. He then worked for the Southeast Asian Fisheries Development Center (SEAFDEC) as a senior research biologist, stationed in Singapore, 1974-1978. He then moved to the Japan Marine Fishery Resource Research Center (JAMARC) in Tokyo in 1979, and engaged in pelagic fish research until 1987. Since then he has been conducting tuna and billfish research at the Far Seas Fisheries Research Laboratory in Shimizu, as a section chief.

James L. Squire, Jr., earned the B.S. degree (marine zoology) in 1950 from San Diego State University, and undertook further graduate studies at the University of California, Los Angeles, in 1951 and 1952. He was marine biologist, California Department of Fish and Game, 1952-1955; assistant chief, then director, north Atlantic fishery exploration and gear research, U.S. Bureau of Commercial Fisheries, 1955-1960; assistant director, then acting director, respectively, Tiburon (California) Marine Laboratory, U.S. Fish and Wildlife Service, 1960-1970, and National Marine Fisheries Service, 1970-1971. Since 1971, he has served as a fishery research biologist, National Marine Fisheries Service, based at La Jolla, California.

8977

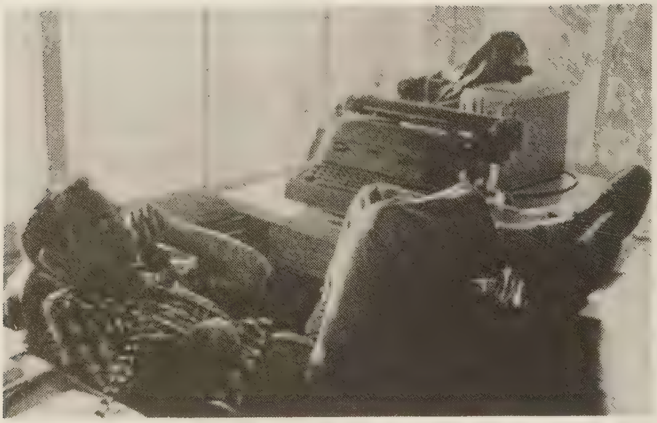
Reuben Lasker:

A REMEMBRANCE

1929 - 1988

THIS ISSUE OF THE Fishery Bulletin *is in memory of Dr. Reuben Lasker who, until his death, was Chief of the Coastal Fisheries Division of the Southwest Fisheries Center, National Marine Fisheries Service. The contributors and I feel both a debt of gratitude and a strong bond of friendship to this scientist who profoundly influenced our investigations, our careers, and the field of marine larval ecology. Our regret is that Reuben will not see this tribute.*

Andrew E. Dizon, Ph.D.
Scientific Editor



It is the spring of 1989 in La Jolla, California, almost a year since our friend and colleague, Reuben Lasker, left us after a valiant battle against cancer. We remember him fondly, with respect and admiration for the man and for the scientist whose intellectual honesty and humanity endeared him to his associates. We, therefore, dedicate this Festschrift to the memory of a remarkable human being, a warm and caring man, who combined a lifelong passion and dedication to the marine sciences with a bright intelligence, a lively curiosity, and an abiding appreciation of the world around us.

Reuben was born in Brooklyn, New York, December 1, 1929, the only child of Theodore and Mary Lasker. As a child he contracted rheumatic fever, and as was customary at that time his doctors prescribed bed rest for an extended period, when Reuben read avidly. The illness, which left Reuben with a slight heart murmur, influenced his activities and increasingly the boy turned to bookish pursuits. He did well in school, attending the prestigious Boys' High School in Brooklyn, graduating at 16. Because of his health, his father decided that Reuben should go to college in Miami, Florida, to escape the rigors of the severe winters in New York. Accordingly, in 1946, Reuben enrolled at the University of Miami as an English major.

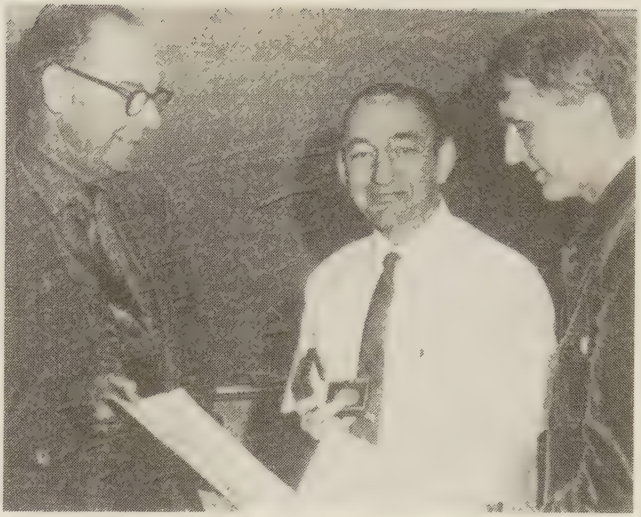
Midway through his college career, Reuben switched his major to zoology with the thought of becoming a medical doctor and in fact actually served as president of the premed society. He received his B.S. degree with honors in zoology, with a minor in chemistry, from the University in 1950. When a graduate research fellowship became available in marine biology, Reuben made a fateful career decision to abandon medicine and applied for the post. He was awarded a full tuition scholarship with stipend for studies in marine biology at the University of Miami where he concentrated on studies on the physiology and cellulose digestion in the shipworm, *Teredo*. He was granted his M.S. in marine biology from the University of Miami in 1952.

Approaching the end of his fellowship at Miami, Reuben began to investigate options for continuing his graduate education. He corresponded with the physiologist, Professor Arthur C. Giese of Stanford University, who had an ongoing marine program at the Hopkins Marine Station. With Giese's encouragement Reuben applied for and was granted a predoctoral fellowship from the National Institute of Health for his doctoral studies at Stanford University. Initially, Reuben was given a small stipend to study the nutrition of the plentiful sea urchins around Monterey Bay. With his young wife, the former Caroline Hayman, the couple drove west in their 1941 black Ford sedan.

Reuben spent the years from 1952 to 1956 on the Stanford campus in Palo Alto researching and writing his doctoral thesis on cellulose digestion in the silverfish. He picked his doctoral topic by chance, although he believed in Pasteur's maxim that chance favors the prepared mind. As Reuben

Opp. page, left: Dr. Gotthilf Hempel of West Germany took this relaxed picture of Reuben during a visit to his laboratory in Building T-21 on the Scripps campus in 1963.

Opp. page, right: Examining a 1 m CalCOFI plankton net in 1965 on the deck of the Bureau of Commercial Fisheries research vessel, *Black Douglas*.



Right: Reuben receiving the U.S. Department of the Interior Silver Medal in 1970 as Gerald V. Howard, Regional Director of the Southwest Region and Alan R. Longhurst, Director of the Fishery-Oceanography Center look on.

was fond of telling the story, he was sitting in a gloomy roomette where the only object left by the former occupant of the cubicle was a box of tissues used in laboratory work. When he reached over and pulled one out, an insect fell down to the table top, skittered away, fell to the floor and disappeared into a crack. The tissue was full of holes and he realized that what he had seen was a silverfish who had made a meal of the paper. Cellulose is difficult to digest by most organisms, and the conventional thought was that animals that eat cellulose, such as the cow or termites, have microorganisms in their stomachs to do the digesting for them. Reuben reflected that since no one had ever mentioned how a silverfish did its cellulose digesting, this might be a suitable topic for a Ph.D. thesis. On completion, the thesis was ranked "Superior" by Stanford University and established Reuben's reputation as an authority on the physiology of this insect. He received his Ph.D. degree in biology in 1956.

In February 1956, Science magazine carried a small announcement in its back pages that a meeting, sponsored by the Rockefeller Foundation, was to be held at the Scripps Institution of Oceanography in La Jolla, California on the future of marine biology. A small amount of money had been set aside for graduate students who were asked to apply to Dr. Adriano Buzzati, the convenor. Reuben promptly wrote to Buzzati, explaining that he was a graduate student at Stanford in marine biology and eminently qualified by inclination and interest to attend. By return mail he received a round-trip ticket from Palo Alto to San Diego and a check for $50 "to cover expenses." At the train station in San Diego, Reuben was picked up by Leo Berner, then a graduate student at Scripps and presently a professor and former dean of oceanography at Texas A&M University, who later became a close friend.

Famous names in marine biology were in attendance at the meeting—Albert Szent-Gyorgyi, Nobel Laureate for the discovery of vitamin C; the English biochemist Ernest Baldwin; Eugene Odum, ecologist from the University of Georgia; Roger Revelle, then the Director of the Scripps Institution of Oceanography and later one of the founders of the University of California, San Diego; John Isaacs, professor of oceanography who was destined to have a profound influence on Reuben; and many others who collectively represented the forefront of research in marine biology, worldwide.

Buzzati, a geneticist, was then a professor at Scripps. He offered to submit a proposal for Reuben to the Rockefeller Foundation to culture euphausiid shrimps, a project on which Reuben had been working. On his return to Stanford, Reuben wrote the proposal and by return mail received notice that he had been awarded a postdoctoral appointment for $5,000 a year (tax-free). By the following September, Reuben and Caroline arrived in La Jolla in a car packed with all their possessions.

The project Reuben chose for himself was to attempt to maintain euphausiids in reasonable health in the laboratory and to find out how effi-

Reuben with Walterio Garcia, Jacobo Melcer, and Paul E. Smith aboard the research vessel *A. Humboldt* in 1975.

Opp. page, left: In foul weather gear aboard the University of Alaska's research vessel, *Alpha Helix*, during a research cruise to the Pribilofs in 1982 to study groundfish.

Opp. page, right: Showing off the Huntsman Medal for Excellence in Biological Oceanography awarded him in 1983 by the Canadian government's Bedford Institute of Oceanography.

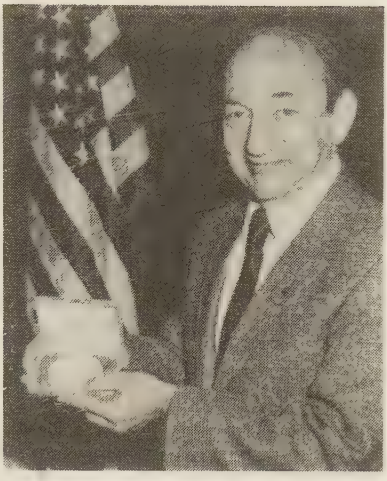
ciently they used their food. Since no one offered to provide him with live animals to work on, Reuben arranged to go to sea on the Scripps T-boat (the U.S. Army's designation for Transportation), an 80-foot vessel with a 3-man crew. Dosed massively with Dramamine, the former Brooklynite who never learned to swim, was taught how to catch euphausiids by Scripps researchers Elizabeth and Brian Boden. During one particularly eventful trip, Reuben was 10 miles off San Diego where the vessel had been stopped to deploy a plankton net. Alone on deck, in heavy seas and without a life jacket, Reuben remembered the ship giving a sudden lurch that propelled him forward over the chain railing. Fortunately for Reuben he managed to save himself by grabbing a projecting object as the ship steamed ahead at 10 knots away from where he would have been hurled into the sea.

Until he finally figured out the correct dosage of Dramamine, Reuben was very susceptible to sea sickness. Although it was necessary to go to sea to collect live specimens, Reuben preferred to keep his sea trips as brief as possible. Serendipitously, he located an area of the ocean in the lee of Pt. Loma which not only produced euphausiids and fish larvae in abundance but also had the virtue of being relatively calm. This became his favorite spot for collecting specimens and in years to come became well known to his colleagues as Lasker's Lake.

The postdoctoral year went quickly with Reuben who was working on the energy balance of euphausiids and looking for a job. A notable event for the Laskers during this time was the birth of their daughter, Pamela.

It was also during Reuben's sojourn at Scripps that a meeting took place which had important implications for his future. Through a mutual friend he met John C. Marr, Director of the U.S. Department of the Interior's Bureau of Commercial Fisheries, South Pacific Fisheries Investigation, who had recently relocated his laboratory in the old Director's residence on the Scripps campus. Marr was interested in Reuben's work on euphausiids, and some months later when the laboratory was reorganized he asked Reuben to head up a physiology section. Meanwhile, Reuben had accepted a job at Compton Junior College; although it provided him with his first taste of teaching, he informed the dean that he would not be renewing his contract because he wanted to return to research. At the end of the academic year, the Lasker family left Compton and returned to La Jolla, where Reuben had been granted a Lalor Faculty Fellowship at the Scripps Institution of Oceanography. In the interim Marr was able to complete the arrangements for Reuben's recruitment. Accordingly, in June 1958, Reuben entered on duty at the federal fisheries laboratory in La Jolla, as a fishery research biologist. Thus began a creative, productive partnership, an association that lasted through numerous federal reorganizations and changes in research emphases, and which endured until Reuben's death some 30 years later.

In establishing a Physiology Program and



selecting Reuben as its principal investigator, Marr embarked on a major change in the direction of research on pelagic marine fishes. He believed that there were many problems that could be solved only through controlled laboratory experiments. Heretofore, few studies had been made on the physiology of pelagic fishes. It had not been possible, for example, to study the fecundity of sardines and other pelagic fishes under laboratory conditions, since fish held in aquaria were not known to spawn. However, under proper conditions of diet or by control of endocrine development, it was at least theoretically possible to induce normal spawning in aquaria. Marr proposed that Reuben undertake such studies as the investigation of the efficiency of food utilization by larval fish, the influence of various factors on the rate of growth, the change in body conditon during ovarian development, and the like.

With this as a mandate, Reuben moved into T-21, one of the gray clapboard cottages (former residences of Scripps' professors) that dotted the hills around Scripps Institution of Oceanography. With the help of his newly hired assistant, Gail Theilacker, a former graduate student at Scripps, he proceeded to establish a laboratory oriented toward basic research, whose main purpose was the study of the innate and adaptive responses of marine organisms. Although Reuben's main academic interest was the investigation of energy exchanges between marine animals and their food supply, he was also interested in other physiological functions that could affect an organism's ability to survive in the sea.

The Physiology Laboratory in T-21 whirred with activity as Reuben threw himself into his new job, infecting others with his customary energy and enthusiasm. Soon, old white bathtubs with clawed feet were filled with seawater and located inside and outside T-21 to hold experimental animals. A particularly robust colony of brine shrimp and algae flourished as a self-contained ecosystem in yet another outside bathtub. One of the first high-speed Beckman ultracentrifuges, used to separate different sardine proteins, hummed upstairs. In another room a continuous oxygen measurement system, using one of the first double electrode probes, which had been invented by Reuben's close friend and colleague, Dr. John Kanwisher, of the Woods Hole Oceanographic Institution, produced quantities of exciting data.

Because government funds were scarce, Reuben took every opportunity to take advantage of federal government surplus property to equip his laboratory for experiments on respiration and energy uptake of sardine eggs and larvae. In the absence of a proper cold room, he located a meat packer's cold locker and set this up outside the building. Another piece of equipment picked up from government surplus lists was a hot dog cooker that had small, rotating aluminum rods to heat the wieners. This, minus the heating element, was adapted by Reuben and Gail to turn syringes filled with sardine eggs rather than wieners. In his enthusiasm to properly study respiration in sardine eggs directly from the sea, Reuben and Gail even installed their Warburg respirometer, without the cooling and shaking system, on the Bureau's old research vessel, the *Black Douglas*, reasoning that the continual shaking motion of the ship would adequately mix the eggs with seawater. Since the work required a constant cold temperature, the only location that met the requirement aboard the *Black Douglas* was deep within the bowels of the ship, accessible only by crawling into the confined space on hands and knees.

It was also about this time that the Cahn electrobalance, now a staple of well-equipped laboratories was developed. The inventor himself set up the equipment in Reuben's T-21 where it was used for weighing individual sardine eggs and larvae. Reuben also took pride that he was one of the first scientists to use the carbon-hydrogen-nitrogen analyzer, and in fact field tested it for the company manufacturing the equipment.

The laboratory soon became a magnet for visiting scientists, investigators, and graduate students. During the summer months, high school students labored at various tasks, measuring euphausiid lengths, collecting limpets, and extracting substances from the tube feet of starfish. From his vantage point at a large wooden desk before a picture window with the panorama of the California coastline curling north, Reuben supervised this activity, while continuing to author or co-author numerous papers on energetics of euphausiids, energetics of sardines, physiology and ecology of fish larvae, and ultimately to studies of the mechanisms underlying recruitment of fishes.

In 1963, Reuben organized a symposium on larval fish biology that would encompass topics ranging from systematics of fish larvae to the technology of fish rearing to the basic physiology of single fish eggs and larvae. In the process Reuben forged close personal and professional links with many of the scientists who attended—James Shelbourne of the Fisheries Laboratory in Lowestoft, England; Gotthilf Hempel of the Institut für Hydrobiologie of the University of Hamburg; J. H. S. Blaxter and F. G. T. Holliday of Aberdeen University; and others—associations which continued throughout his life.

In 1966, Reuben and his family, which now also included a son, Paul, traveled to Aberdeen, Scotland to work at the University of Aberdeen for one year with Blaxter and Holliday. Here Reuben applied the techniques perfected in his work on euphausiid shrimps to the study of the food chain in an experimentally developed fishery, utilizing hatchery-reared larval and juvenile plaice. The year in Scotland with his family proved to be one of the happiest in Reuben's life, leaving him with an abiding affection for all things Scottish.

In October 1964, the Bureau of Commercial Fisheries, Fishery-Oceanography Center, as it was then called, was completed, adjacent to the campus of the Scripps Institution of Oceanography. It was an imposing structure of four concrete buildings grouped around a central courtyard, 220 feet above the Pacific Ocean. The gray cottage, T-21, site of many research accomplishments, was abandoned. Reuben and his staff moved into a wing of the Center which was equipped with the most modern equipment and perhaps most importantly gave access to an experimental seawater aquarium with temperature control rooms for physiological studies and rearing experiments, all of which Reuben helped to design.

With the move into his well-equipped new laboratory, Reuben assembled a dedicated cadre of behaviorists, physiologists, oceanographers, population dynamicists, and experimental biologists. At this point in his professional life he had already established a solid basis of scientific achievement on which others could build. His work on the energy exchange between fishes and their food supply, his work on osmoregulation by sardine embryos and larvae, and his work on the effect of temperature on the growth and development of both sardine and anchovy larvae were fundamental to understand the dynamics of fish populations and provided the scientific rationale for the project to rear pelagic marine fish in the laboratory. Subsequently, under Reuben's direction and leadership, more than 30 species of pelagic fishes, including the commercially valuable sardine, anchovy, and mackerels, were reared from eggs, through larvae, to subadult stages, for the first time ever in a laboratory. Reuben's papers on marine invertebrates and on the energy budget of clupeids in relation to their planktonic food were widely read and quoted. His paper on the feeding, growth, respiration, and carbon utilization of a euphausiid crustacean became a citation classic (Current Contents, 1983, Volume 14, page 17).

With outstanding researchers and equipment, particularly the facilities of the experimental seawater aquarium, at his disposal, Reuben was able to concentrate his research on ecological and physiological factors that would help answer one of the most important and fundamental questions in fisheries: What determines how many young fish will survive the rigors of life in the sea to become reproducing adults?

Ever the creative and imaginative scientist, Reuben constantly came up with fresh and innovative scientific approaches. An example was an experiment in which he took anchovy larvae spawned in the Center's seawater aquarium to sea in order to test his idea that laboratory-raised anchovy could be used in lieu of naturally spawned larvae as an assay of conditions in the sea.

Another remarkable idea came to Reuben when he was on a cruise to sample patches of larval food. Following a storm with strong winds that mixed and diluted the dense layer of larval forage from which he had drawn his samples, it occurred to him that upwelling events and storms are detrimental to fish larvae because these events dilute concentrations of larval food. He suggested that larval survival increases during periods of weak winds when the coastal seas stratify and the forage of larval fishes concentrates in layers. This "stability" hypothesis has greatly interested oceanographers and fishery biologists both in this country and abroad and has stimulated efforts of individual researchers to study the definitive links between fish larvae and their microenvironment. Now known as "Lasker Events" (see following article on "An eponym for Reuben Lasker" by Daniel Pauly), these calm periods could be the key factor in larval survival, and ultimately recruitment.

The years passed quickly and happily for Reuben. As Chief Scientist of what would become the Coastal Fisheries Resources Division, he directed the efforts of a multidisciplinary research team and was signally successful in stimulating and inspiring his staff to pursue promising avenues of research. This record of research achievement received mention in the review conducted by the National Academy of Sciences in its evaluation of the National Oceanic and Atmospheric Administration's ocean research and development. The examiners wrote, "The Coastal Division represents a center of excellence . . . the Division has a high scientific awareness, much talent and enthusiasm, and is doing some excellent research."

One remarkable example of how Reuben's leadership and influence led to a major breakthrough is his role in developing the estimation procedure for anchovy biomass assessment. He was among the first to recognize the unique potential of this method and was responsible for bringing together the disparate disciplines and people that made it work. The method permits the estimate of biomass from the ratio of the egg production rate in the sea to the daily fecundity of the spawning fish stock. This new method of pelagic population analyses was accomplished by a team effort and was founded almost entirely on previous research done by Reuben and others, research which provided the essential background information on which to build. In order to develop the anchovy biomass assessment, a wide variety of studies on sampling, statistical methodology, fish biology, ecology, behavior, and physiology had to be made. All of these studies added greatly to the knowledge of clupeoid biology.

As of this writing, the biomass assessment method has been incorporated into the Northern Anchovy Management Plan as a guide for setting anchovy fishing quotas in the coastal waters of the U.S. Pacific Coast and has been adapted in other countries such as South Africa and Peru. It is increasingly viewed by many fisheries scientists as the best current assessment technique for fishes with pelagic eggs.

In 1970, in response to a request from the administrators of the fisheries service, Reuben (with the able assistance of the late Lon Manar as the managing editor) undertook the task, as scientific editor, of revitalizing the venerable U.S. *Fishery Bulletin*. Before 1971, the Fishery Bulletin appeared irregularly for lack of sufficient contributions of merit. Authors sought other journals because it took 2–3 years to get papers published in the Fishery Bulletin. During Reuben's first year as editor, the Fishery Bulletin became a quarterly and the number of pages printed per year almost tripled. Because of his scientific reputation, Reuben was able to attract to the pages of the Fishery Bulletin not only outstanding contributions from members of the NMFS staff but also major contributions from scientists outside NMFS. He initiated and enforced a peer review system for reviewing manuscripts, not only for the Fishery Bulletin but also for other NMFS publications. His impact on the scientific image, character, and tone projected by NMFS publications was a reflection of his own standards of scientific excellence and personal integrity. The revitalized Fishery Bulletin, an indispensable research journal to those in the field of fisheries, now reaches several thousands of readers worldwide. Reuben's contributions as Scientific Editor were even more remarkable becaues he worked at this job only half-time while continuing his research on fish physiology.

Reuben also served as an essential link to the surrounding academic community, particularly the nearby Scripps Institution of Oceanography with which the fisheries laboratory had long maintained close ties. In 1966 he received an appointment as an Associate Professor of Marine Biology in Residence at Scripps and in 1973 was appointed Adjunct Professor of Marine Biology. He supported and encouraged his graduate students, and participated with his usual enthusiasm in faculty committee work. It was most typical of Reuben that although his strength was sapped by his illness he introduced his last graduate student at a thesis defense several days before his death with humor and wit.

During his 30 years as a government scientist he put together many workshops and meetings which attracted scientists from all over the world and fostered creative collaborative efforts. For example, in recent years, he organized workshops for the Sardine-Anchovy Recruitment Program (SARP) which brought together scientists from all major upwelling regions of the world to develop a practical plan for studying recruitment. Major credit for the active and productive SARP programs that exist today in many parts of the world belongs to Reuben's efforts and interest.

He was a gregarious man who loved people and conversation. He delighted in travel to the far places of the world. Many of the letters received after his death testify eloquently to the warm affection and regard in which he was held by hundreds of his colleagues throughout the world.

During his lifetime Reuben was the recipient of high honors. The U.S. Government awarded him the Meritorious Service Award of the U.S. Department of the Interior (Silver Medal Award) in 1970 and the Distinguished Service Award of the U.S. Department of Commerce (Gold Medal Award) in 1974. The Canadian Government's Bedford Institute of Oceanography awarded him the Huntsman Medal for Excellence in Biological Oceanography in 1983.

Reuben's preeminent role as outstanding researcher, his practical wisdom, wide experience, and knowledge made him much sought after as a prime mover, advisor, and member of many prestigious committees, commissions, and boards where he served with distinction, most recently as a member of the Ocean Studies Board of the National Academy of Sciences.

He maintained close ties with friends and colleagues around the world, through voluminous correspondence and telephone calls. He was ever the optimist and many of his correspondents never realized the gravity of his illness which re-occurred in March of 1987. As his lifelong close friend, Dr. Howard Feder of the University of Alaska wrote later, "I can hear Reuben's voice in my head saying, 'Goodbye, old buddy. Don't be sad. I did everything I wanted; I have no regrets. Remember, Howie, life goes on! Enjoy yourself.'" On April 27, 1988 his friends scattered his ashes from the National Marine Fisheries Service research vessel, *David Starr Jordan*, appropriately enough, in the sea off Point Loma, known as Lasker's Lake.

For those of us lucky enough to have shared this life with him, the thought of Reuben will always bring the warmest memories. As his friend Lucian Sprague wrote, "As long as there are friends who remember him, students to read his papers and to carry on his work, he will be very much with us in spirit."

In the year which followed Reuben's death, his friends organized the Reuben Lasker Memorial Fund. The Fund is administered by the Coordinator of the California Cooperative Oceanic Fisheries Committee (CalCOFI) and is used for travel fellowships for students to attend the annual CalCOFI meeting. Anyone interested in contributing to the fund may do so by writing to the CalCOFI Coordinator, P.O. Box 271, La Jolla, CA 92038. Also in 1988, the American Institute of Fishery Research Biologists posthumously awarded Reuben their Outstanding Achievement Award for his distinguished lifetime career accomplishments in fisheries science and for his outstanding contributions to research and management.

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An Eponym for Reuben Lasker

Reuben Lasker published in 1975 and 1978 two papers in which he suggested that the maintenance—through a "period of calm"—of thin layers of food-rich patches was crucial to the survival of newly hatched northern anchovy larvae. These papers had an enormous influence on fisheries research throughout the 1980s, as can be easily assessed, e.g., through citation analysis.

Recently, Peterman and Bradford (1987, their note No. 16) operationally defined the periods of calm alluded to above as periods of four consecutive days with wind speed below 10 m s^{-1}. They also proposed to view periods of five consecutive calm days as two partly overlapping 4-day periods, period of six days as three partly overlapping periods, etc.

I recently proposed (Pauly 1987), in a book largely devoted to following up on R. Lasker's work, the term "Lasker events" as an eponym for a period of four calm days with winds less than 5 m s^{-1}. The present volume provides an appropriate context to reiterate and refine this suggestion.

Thus, to allow different authors to identify different hypotheses related to the effects of periods of calm, I propose to use the notation "*i/j* Lasker event" for period of calm lasting i days and defined by winds not exceeding $j \text{ m s}^{-1}$. Thus, e.g., Peterman and Bradford (1987) worked with "4/10 Lasker events", while Mendelssohn and Mendo (1987) worked with "4/5 Lasker events".

This suggestion offers a parallel for the more general "Lasker-hypothesis" now widely used as an eponym for the mechanism proposed by Lasker (1978, 1985).

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8978

Larval Production and Mortality of Pacific Saury, *Cololabis saira*, in the Northwestern Pacific Ocean[1]

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ABSTRACT: Because quantitative samples of saury eggs are difficult to obtain owing to their adhesive nature, reproductive level of the Pacific saury, *Cololabis saira*, has been estimated from the standing stock of the larvae and juveniles in Japan. Mortality curves were constructed and daily larval production at hatching was estimated for combined data from 1972 to 1986 and for consecutive individual years within this period. Durations of size classes were estimated from a growth curve and used to calculate fish production at age. Because number of fish captured by a net tow (area = 401.3 m^2) showed a diel cycle due to fish behaviors, such as net frame evasion and diel vertical movement, the average mortality curve for 15 years was based on data collected at night. We used an exponential decay model to describe the mortality of saury larvae and juveniles. The daily instantaneous mortality rate was 0.078, and the larval production at hatching was 1.255 larva/tow/day. Mortality curves for the individual years were based on data collected throughout the day and night after correction by size- and time-specific retention rates. Daily larval production at hatching fluctuated among individual years ranging from 0.154 to 5.176. Daily instantaneous mortality rates positively correlated with larval production at hatching, which might indicate the presence of a density-dependent process in larval mortality.

Together with the Japanese sardine, *Sardinops melanosticta*, and the mackerels, *Scomber japonicus* and *S. australasicus*, the Pacific saury, *Cololabis saira* (Brevoort), is one of the most important offshore pelagic fishes in Japan. Although total catch of the saury in Japan (210,000 t [metric tons] in 1984) was much smaller than that of the sardine (4,180,000 t) or the mackerels (810,000 t) (Statistics and Information Department, Japan 1986), more than 95% of the catch is destined for human consumption (Japan Saury Fishery Association 1985). In sharp contrast, the sardine (81%) and the mackerel (40%) catches (Fisheries Agency 1985) are procesed for animal foods.

Saury fishermen in Japan expect to have a reliable fishing forecast provided by the Tohoku Regional Fisheries Research Laboratory, Fisheries Agency of Japan, every summer before the beginning of the fishing season. The forecast includes the expected catch in the coming season and the potential fishing grounds. The expected catch depends on fish stock size, and the location and size of the fishing grounds are a function of fish migration in relation to oceanographic conditions. Fish stock size is determined by both reproductive level and mortality rates of developmental stages from postspawning through recruitment. Since the saury grows rapidly and becomes an adult within one year (Watanabe et al. 1988), larval production and mortality rate in young stages are believed to be more or less directly related to recruitment and catchable stock size. Matsumiya and Tanaka (1978) suggested from their intensive study of population dynamics of the northwestern Pacific saury that the fluctuations of population size are seriously affected by reproductive success.

An egg survey may be the best method for estimating the reproduction level of pelagic fishes. However, it is difficult to conduct a quantitative egg survey of the saury by towing plankton nets because the eggs attach by filaments to floating objects such as drifting kelp. We therefore have been conducting larval and juvenile surveys to estimate the reproductive level. We use catch/tow (number of fish/net tow) values of several size classes as abundance indices. The year-to-year changes of the indices may reflect the fluctuation of reproductive level.

The apparent number of larvae in a size class is influenced by the duration of growth through that size class. If growth is slow, the duration will be extended; conversely, if growth is fast, the duration will be short. The duration of growth through a size class thus defines the

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amount of time that larvae or juveniles are vulnerable to capture. Because the growth rate is not constant over the size range of the young fish sampled in this study, we must correct for this bias. The production of larvae by age is defined as the abundance of larvae by size divided by the duration of growth through the size class, which is expressed as catch/tow/day. This allows us to calculate instantaneous mortality rate (IMR), and thus, construct a mortality curve. We need to know age and growth rate of saury to calculate production at age and mortality rates.

In northern anchovy, *Engraulis mordax*, there have been extensive studies of eggs and larvae, and the methods to calculate the production and mortality rate were established (Zweifel and Smith 1981; Lasker 1985; Lo 1985; 1986). Ichthyoplankton survey data, embryonic incubation times, and larval growth rates are the essential parameters for this method. Further, one needs to have information on possible biases of tow data. For the Pacific saury, we have 15 years of larval net-tow data, a newly developed growth model based upon otolith growth increments (Watanabe et al. 1988), and information on bias correction of tow data for day and night differences. All these make it possible to compute fish production at different ages and mortalities. Extending the mortality curve to age 0, we can calculate larval production at hatching, which might be the best index of reproductive level so far available. In this paper we selected the exponential decay mortality curve and used it to calculate the larval production at hatching and the daily IMR of Pacific saury in the northwestern Pacific Ocean for 1972–86.

METHODS

Data Source

The Pacific saury spawns nearly all year round in the entire northwestern Pacific Ocean. The sampling areas and seasons were somewhat different from year-to-year, but our data set of 15 years (1972–86) included around-the-clock samples taken all year from a large area of the northwestern Pacific, lat. 29–45°N, long. 129–174°E (Fig. 1).

Saury larvae and juveniles were collected by a surface ring net that was towed for 5 minutes at 2 knots. The mouth diameter was 1.3 m, and therefore the surface area covered by one tow was 401.3 m^2. A mesh size of the 3.0 m forward part of the net was 2.0 mm, and the 1.5 m rear part was 0.33 mm. Samples were washed down after the 5 min tow and preserved in 10% unbuffered formalin. Larvae and juveniles of saury were measured to the nearest 0.1 mm knob length (KnL), the distance from the tip of the lower jaw to the posterior end of a muscular knob at the base of the caudal peduncle. They were then grouped into 11 size classes from 7.5 mm (including 5.0–9.9 mm) up to 57.5 mm (55.0–59.9 mm). The midpoint and both limits of each class were then converted into the capture size before preservation, using a shrinkage factor by formalin preservation (0.97) reported by Theilacker (1980) for northern anchovy. The midpoint of each size class was used to represent the class, though it is not a mean age of the class. The capture size was converted to age, and duration of each size class was obtained using the growth model developed by Watanabe et al. (1988). The growth equation from hatching to a 100 mm juvenule is

$$\mathrm{KnL} = 5.90 \exp((0.0865/0.0293) \times (1 - \exp(-0.0293\, t)))$$

where KnL is the fish knob length in mm after capture (before preservation) and t is the age in days from hatching.

Bias Corrections

An ichthyoplankton survey is essential for most pelagic fish research (Smith and Richardson 1977), but it is not bias free. The most common biases in catch of fish eggs and larvae are extrusion of eggs and larvae through net mesh and evasion of a net frame by fish. For the Pacific saury, the mesh size of the anterior part of the net, 2.0 mm, might be large enough to lose larvae by extrusion. Vulnerability of the fish to a net tow varies throughout a day due to changes in evasion abilities. Availability of the fish to a tow changes as well due to diel vertical movement. These factors result in differences in numbers of fish captured by net tows during the day and night. For the analysis, we defined 10 diel time periods based upon angles between the center of the sun and the celestial horizon. We used four periods in the morning—DAWN (DWN), MORNING TWILIGHT (MTW), SUNRISE (SRS), and MORNING (MRN)—and another four periods in the evening—AFTERNOON (AFT), SUNSET (SST), EVENING TWILIGHT (ETW), and DUSK (DSK). Time dura-

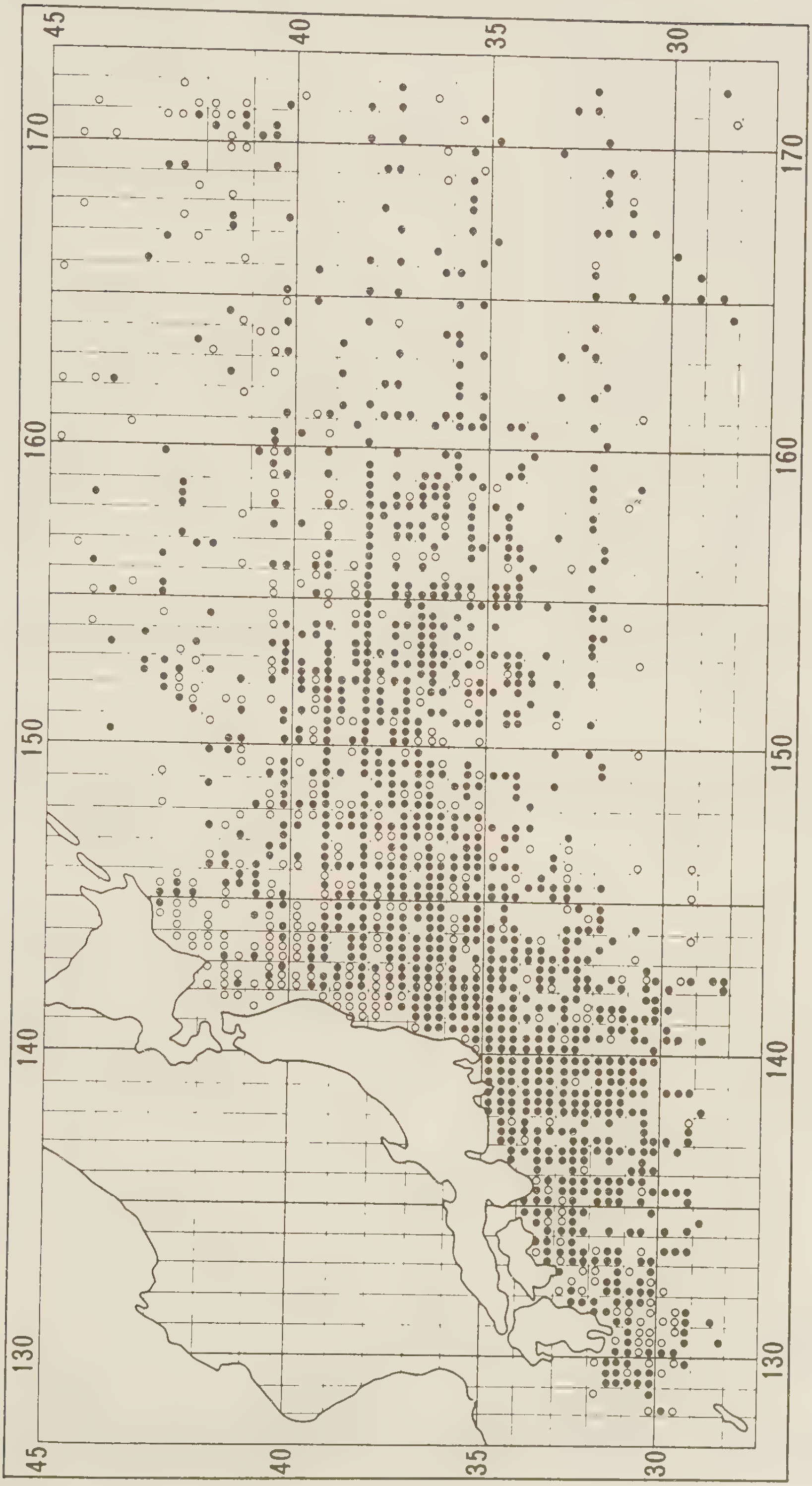

FIGURE 1.—Composite survey area of Pacific saury larvae and juveniles in the northwestern Pacific Ocean, 1972–86. Solid (open) circles represent areas where a positive tow has ever (never) been recorded in the period.

tion between the end of MRN and the beginning of AFT was named DAYTIME (DAY), and the time duration between the end of DSK and the beginning of DWN was named NIGHTTIME (NIT). We examined the data collection of 15 years (1972–86) and estimated size- and time-specific retention rates. Changes of these values are due to the fish behaviors such as net frame evasion and vertical migration. The rates were calculated by taking ratios of catch/tow in each time category and that of the NIT (Table 1). Extrusion of larvae was examined as well, comparing observed numbers of fish with predicted numbers calculated from a mortality curve (see results section for detail).

To reduce the seasonal effect of larval production and mortality, we also considered the bias on average catch/tow within a year from unproportional sampling efforts among months. Net tows were concentrated between February and May; the percentage of juvenile fish in the total catch was low in winter and increased in spring and early summer (Fig. 2). Thus, we divided 12 months of the year into 4 seasons based upon the abundance of saury larvae and juveniles: January to March as the main spawning season, April to June as the late spawning season, July and August as the off spawning season, and Sep-

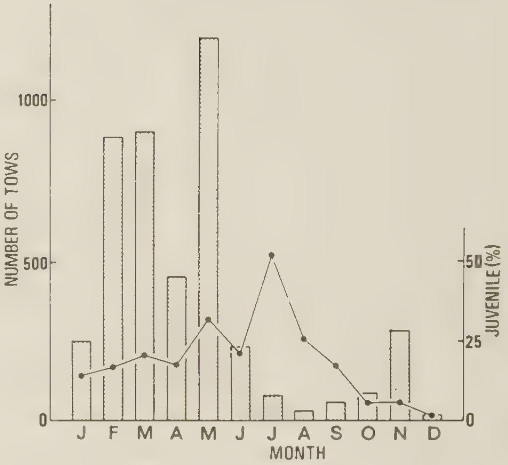

FIGURE 2.—Number of tows (columns) and percentage of juvenile Pacific sauries (dots) in total fish captured by months.

TABLE 1.—Annual average of Pacific saury catch/tow (c/t) and size- and time-specific correction factors (CF) of size classes in 10 time categories.

Time category (# tows)	Size class (mm):	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
SRS	c/t	1.115	1.495	0.330	0.065	0.260	0.021	0.011	0.005	0.026	0.021	0.058
(92)	CF	0.864	0.724	0.220	0.072	0.475	0.064	0.050	0.029	0.215	0.158	0.450
MRN	c/t	1.588	2.281	0.521	0.352	0.154	0.043	0.039	0.028	0.019	0.003	0.000
(165)	CF	1.231	1.104	0.348	0.390	0.282	0.131	0.176	0.165	0.157	0.023	—
DAY	c/t	1.400	1.134	0.509	0.209	0.098	0.042	0.034	0.008	0.002	0.002	0.016
(1,517)	CF	1.085	0.549	0.343	0.232	0.179	0.128	0.154	0.047	0.017	0.015	0.124
AFT	c/t	2.090	2.004	1.022	0.403	0.176	0.039	0.018	0	0	0	0.003
(199)	CF	1.620	0.970	0.682	0.447	0.322	0.119	0.081	—	—	—	0.023
SST	c/t	1.486	1.175	0.937	0.501	0.524	0.189	0.006	0	0	0	0
(97)	CF	1.152	0.569	0.626	0.555	0.958	0.578	0.027	—	—	—	—
ETW	c/t	0.422	0.782	0.393	0.218	0.133	0.079	0.070	0.031	0.017	0.014	0.007
(132)	CF	0.327	0.379	0.262	0.242	0.243	0.242	0.317	0.182	0.140	0.105	0.054
DSK	c/t	1.425	1.700	1.354	0.867	0.641	0.268	0.340	0.428	0.192	0.121	0.084
(218)	CF	1.105	0.823	0.904	0.961	1.172	0.820	1.538	2.518	1.582	0.910	0.651
NIT	c/t	1.290	2.066	1.498	0.902	0.547	0.327	0.221	0.170	0.121	0.133	0.129
(1,805)	CF	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
DWN	c/t	0.803	1.465	1.285	0.750	0.499	0.313	0.205	0.152	0.082	0.088	0.053
(203)	CF	0.622	0.709	0.858	0.831	0.912	0.957	0.928	0.894	0.678	0.662	0.411
MTW	c/t	0.568	0.610	0.434	0.250	0.158	0.053	0.026	0.046	0.020	0.092	0.020
(80)	CF	0.440	0.295	0.290	0.277	0.289	0.162	0.118	0.271	0.165	0.692	0.155

[1] SRS = SUNRISE; MRN = MORNING; DAY = DAYTIME; AFT = AFTERNOON; SST = SUNSET; ETW = EVENING TWILIGHT; DSK = DUSK; NIT = NIGHTTIME; DWN = DAWN; MTW = MORNING TWILIGHT.

tember to December as the early spawning season (Fig. 3). We calculated catch/tow values of 4 seasons separately in every size- and time-group by summing up the number of fish and net tows of 15 years and then taking average catch/tow values of 4 seasons. These values, average catch/tow values of the year, were used for calculation of the size- and time-specific retention rates mentioned above.

Mortality Models and Computations

The mortality model of the young saury from hatching (age 0) to 52 days old (57.5 mm preserved KnL) was based on the data of catch/tow/day (daily production) at ages. Two types of mortality curves were fitted to both the combined data collected in the NIT period for 1972–86 and the data set from 14 individual spawning years. One mortality curve is based on an age-dependent instantaneous mortality rate (IMR), $Z_1(t) = \beta/t$, and the other based on the age-independent constant IMR, $Z_2(t) = \alpha$, where t is the fish age in days and α and β are coefficients of IMR. The age-dependent IMR was considered because of the possibility that early larvae may suffer higher mortality than the older ones, as in the case of northern anchovy larvae along the California coast (Lo 1985, 1986). We constructed both mortality curves for saury larvae and juve-

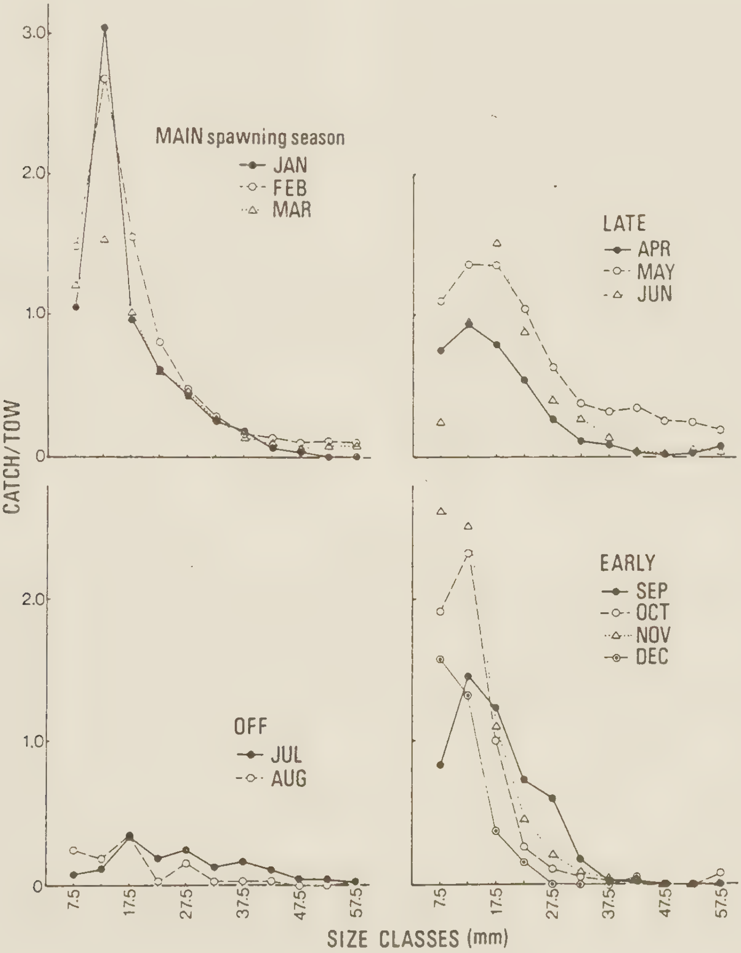

FIGURE 3.—Division of the year into four spawning seasons based on the number of Pacific sauries captured by a net tow (catch/tow) by months.

niles. The mortality curves based on $Z_2(t)$ fitted the larval and juvenile data better than $Z_1(t)$, and therefore, we chose $Z_2(t)$ to describe the fate of young sauries. The mortality curve with a constant IMR takes the form of the exponential mortality curve,

$$P_t = P_0 \exp(-\alpha t)$$

where P_t is the daily fish production at age t, t is the age in days from hatching, P_0 is the daily larval production at hatching, and α is the daily IMR.

For the computation of larval production and mortality rate averages of 15 years, we used the data of the NIT category. For the computations of individual years, however, the number of NIT samples were not sufficient; therefore, we had to use the data from all the time periods. The data sets of individual years were classified into 10 time periods of 11 size classes and were corrected by dividing numbers of fish by their specific retention rates (Table 1). The corrected numbers of fish were summed up in each size class and divided by the total number of tows of the year to calculate catch/tow values as the abundance index of each size class.

We used the catch data of the early, main, late, and off spawning seasons (from September to August of the following year) as a unit of a spawning year instead of the calendar year. According to the recent growth model by Watanabe et al. (1988), the saury becomes adult within a year, so, we supposed that the larvae produced in a spawning year constitute the major part of the year class of the current year.

The catch/tow value of each size class was further divided by the duration of the corresponding size class. This provided the production rate (catch/tow/day), which was used for the computation of larval production at hatching and mortality. The parameters, larval production at hatching (P_0) and daily IMR, are estimated by using a nonlinear program (Par (Dixon et al. 1985)).

RESULTS

The Overall Mortality Curve for 1972–86

To understand the fate of young sauries from 1972 to 1986, the average catch/tow/day from the NIT samples (Table 2) was used to estimate the larval production at hatching and the IMR. All the fish were first grouped into 11 size classes, ranging from 7.5 mm (5.0–9.9 mm) to 57.5 mm (55.0–59.9 mm), and the midpoint of each size classes was converted to age. The data from the first two size classes (7.5 mm and 12.5 mm) were excluded from the analysis because the catch/tow/day in these two size classes was lower than the next older larvae. The downward bias could be due to extrusion of the larvae through the mesh. The estimates of the larval production at hatching (P_0) and daily IMR were 1.255 larvae/tow/day (SE = 0.111) and 0.078 (SE = 0.004), respectively (Fig. 4). The total daily mortality rate $((P_{t-1} - P_t)/P_{t-1} = 1 - (\exp(-\alpha)))$ was 7.5% from the newly hatched larvae to the 52 d old juvenile.

TABLE 2.—Daily production (catch/tow/day) at age (day) of Pacific saury from NIGHTTIME samples, 1972–86.

Midpoint size (mm)	pr[1]	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
	cp[2]	7.7	12.9	18.0	23.2	28.4	33.5	38.7	43.8	49.0	54.1	59.3
Age (day)		3.2	10.5	16.2	21.3	25.9	30.3	34.5	38.8	43.1	47.4	52.0
Size range (mm)	pr	5.0–	10.0–	15.0–	20.0–	25.0–	30.0–	35.0–	40.0–	45.0–	50.0–	55.0–
	cp	5.2–	10.3–	15.5–	20.6–	25.8–	30.9–	36.1–	41.2–	46.4–	51.5–	56.7– 61.8
Stage duration (day)		7.1	6.4	5.3	4.9	4.4	4.3	4.2	4.3	4.3	4.4	4.7
# fish observed		2,030	3,982	3,352	2,148	1,333	821	536	406	330	375	351
Catch/tow		1.125	2.206	1.857	1.190	0.739	0.455	0.297	0.225	0.183	0.208	0.194
Daily fish production		[3]0.158	[3]0.345	0.350	0.243	0.168	0.106	0.071	0.052	0.043	0.047	0.041

[1] Fish knob length after preservation.
[2] Fish knob length after capture (before preservation).
[3] Not used for the computation.

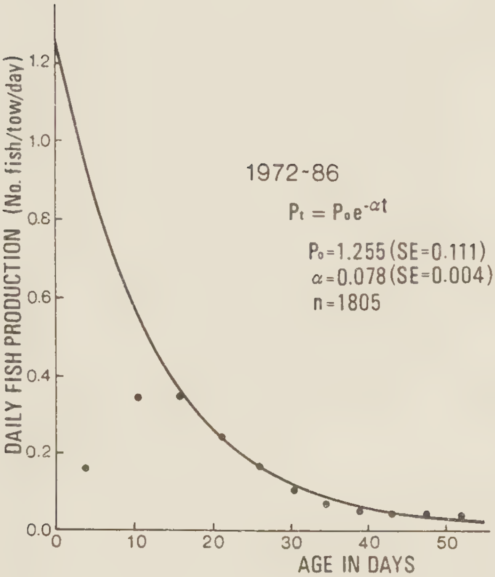

FIGURE 4.—Mortality curve of young Pacific saury calculated from fish production at ages calculated from the NIT data of 15 years (1972–86). Data points of the smallest two size classes were not used for the computation. P_0 is the larval production at hatching, α is the daily IMR, and n is the number of tow samples.

Mortality Curves for Individual Spawning Years

To assess the mortality of young saury for individual spawning years, we used all the tow data collected around the clock, after the correction of catch data by the size- and time-specific retention rates (Table 1). The correction procedures are the same for all the spawning years. To illustrate the data assemblage and computation, the 1979 catch data set for 11 size classes was given (Table 3). Again, the data points of the first two size classes were not used in the estimation procedure because of the apparent downward bias. The parameter estimates and the mortality curves are summarized in Table 4, and the mortality curves are presented in Figure 5.

The larval production at hatching (P_0) fluctuated by more than 30-fold from the maximum 5.176 larvae/tow/day in 1978 to the minimum 0.154 in 1985 spawning year. Daily IMR has also ranged from 0.115 down to 0.041, with daily mortality rates of 10.9% and 4.0%, respectively.

Year-to-year fluctuations of these two parameters (P_0 and IMR) and the total catch of saury in Japan (Statistics and Information Department, Japan 1987) are presented in Figure 6. The total catch of saury can be an index of the stock size, though possibly including effects of economic factors such as fish price. The fishing season of saury opens in the first half of August and closes in the middle of December. Since the saury becomes adult in 9–10 months and 2 yr old fish were not found in the northwestern Pacific

TABLE 3.—Daily production (catch/tow/day) at age (day) of Pacific saury in 1979 spawning year (September 1978–August 1979).

Midpoint	pr[1]	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
size (mm)	cp[2]	7.7	12.9	18.0	23.2	28.4	33.5	38.7	43.8	49.0	54.1	59.3
Age (day)		3.2	10.5	16.2	21.3	25.9	30.3	34.5	38.8	43.1	47.4	52.0
Size	pr	5.0–	10.0–	15.0–	20.0–	25.0–	30.0–	35.0–	40.0–	45.0–	50.0–	55.0–
range (mm)	cp	5.2–	10.3–	15.5–	20.6–	25.8–	30.9–	36.1–	41.2–	46.4–	51.5–	56.7–61.8
Stage duration (day)		7.1	6.4	5.3	4.9	4.4	4.3	4.2	4.3	4.3	4.4	4.7
# fish observed		607	1,267	738	420	194	68	61	32	16	13	9
# fish corrected		674	1,470	939	625	245	98	90	62	22	14	10
Catch/tow		1.685	3.676	2.349	1.562	0.613	0.244	0.226	0.155	0.054	0.036	0.026
Daily fish production		[3]0.236	[3]0.574	0.443	0.319	0.139	0.057	0.054	0.036	0.013	0.008	0.006

[1] Fish knob length after preservation.

[2] Fish knob length after capture (before preservation).

[3] Not used for the computation.

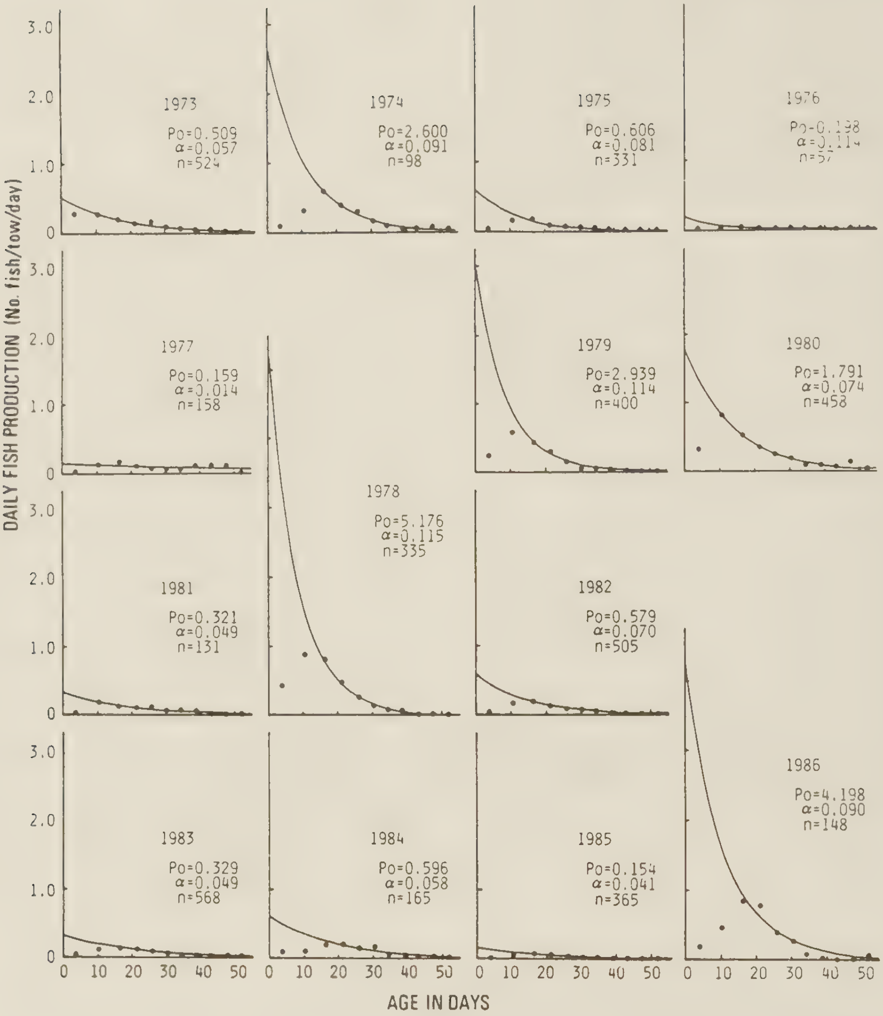

FIGURE 5.—Mortality curves of individual spawning years. P_0 is the Pacific saury larval production at hatching, α is the daily IMR, and n is the number of tow samples.

(Watanabe et al. 1988), the total catch in a fishing season must come from larvae produced in the spawning period of the same year. For example, the 1973 catch is related to larval production at hatching and daily IMR of the 1973 spawning year (from September 1972 to August 1973).

Larval production at hatching and the daily IMR have fluctuated somewhat concordantly from 1973 to 1986. The Spearman's Rho is 0.704 ($n = 14$, $P < 0.05$), indicating a positive correlation between P_0 and IMR among years. The exception to this trend was 1976. The production value of 1976 was one of the lowest in 14 years whereas the daily IMR was very high, probably resulting in a minimum catch of <100,000 t in 1976.

Mesh Retention of Larvae

The low values of larval production for the first two size classes precluded their use in the estimation of larval mortality. Since the mesh size of the anterior 3.0 m of the net is 2.0 mm, we

TABLE 4.—Daily larval production at hatching (P_0) and daily instantaneous mortality rates (IMR) of individual spawning years with standard error in parentheses.

Spawning year	P_0 (larva/tow/day)	IMR	Mean square error ($\times 10^{-4}$)
1973	0.509 (0.100)	0.057 (0.008)	4.05
1974	2.600 (0.410)	0.091 (0.007)	10.20
1975	0.606 (0.112)	0.081 (0.009)	1.37
1976	0.198 (0.080)	0.114 (0.022)	0.13
1977	0.158 (0.067)	0.014 (0.013)	19.00
1978	5.176 (0.433)	0.115 (0.004)	3.33
1979	2.939 (0.653)	0.114 (0.012)	8.02
1980	1.791 (0.284)	0.074 (0.007)	12.50
1981	0.321 (0.100)	0.049 (0.012)	6.00
1982	0.579 (0.084)	0.070 (0.006)	1.36
1983	0.329 (0.055)	0.049 (0.007)	1.83
1984	0.596 (0.213)	0.058 (0.015)	17.10
1985	0.154 (0.037)	0.041 (0.009)	1.30
1986	4.198 (1.325)	0.090 (0.015)	104.00

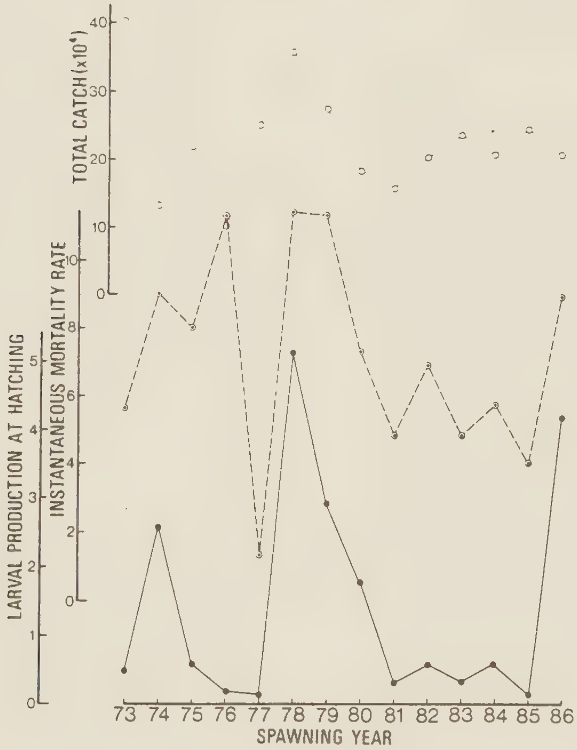

FIGURE 6.—Year-to-year fluctuations of daily Pacific Saury larval production at hatching in number of larvae per tow (——●——), daily IMR (-----⊙-----), and the annual total catch in metric tons (-----○-----) of the saury.

think that the downward bias is due to extrusion through the mesh. The mesh retention rate of larvae in the first two size classes could be estimated from the ratio of the observed catch/tow/day and the predicted larval production computed from the overall average mortality curve of 15 years. The estimate of mesh retention rate for larvae of 7.5 mm (3.2 days old) is,

Observed: 0.158 (larvae/tow/day)
Predicted: 0.978 (larvae/tow/day) = 1.255 $\exp(-0.078 \times 3.2)$
Retention rate: 0.16 = 0.158/0.978

and for larvae of 12.5 mm (10.5 days old) is,

Observed: 0.345 (larvae/tow/day)
Predicted: 0.553 (larvae/tow/day) = 1.255 $\exp(-0.078 \times 10.5)$
Retention rate: 0.62 = 0.345/0.553.

DISCUSSION

Production and mortality rates of fish larvae and juveniles cannot be obtained without good growth models, which are indispensable in calculating stage durations. A new growth model based on growth increments of otoliths has recently been established (Watanabe et al. 1988) enabling calculation of mortality rates. The current results are virtually the first attempt to calculate larval production at hatching. These should provide the best index of reproductive level ever obtained.

Sablin (1978) first calculated mortality rate of juvenile saury for 8 individual years (1968–75), using catch/tow values of two size groups, 26–30 mm and 46–50 mm, and 20 mm/mo as a growth rate of this size range. The average monthly IMR estimated by Sablin was 1.15 with a range from 0.76 to 1.62. He obtained the IMR from 2 size groups for individual years, whereas we used catch data from 9 size classes in computing the IMR. We believe the estimates of IMR reported here are an improvement over those of Sablin.

Monthly mortality rates using the Sablin IMRs (1978) ranged from 53.2% to 80.2% with an average of 68.3%. These values were much lower than the monthly rates calculated from the daily IMRs in this paper, 70.8–96.8% with an average 90.4%. The discrepancy between the two seems to derive from the difference in growth rates used for the computations (Fig. 7). Sablin used a rate of 20 mm/mo (0.67 mm/d) for the size range from 26–30 mm to 46–50 mm. We used the growth model by Watanabe et al. (1988), which shows that sauries grow from 27.5 mm to 47.5 mm in 17.2 days (1.16 mm/d). This was 1.7 times faster than growth rate of Sablin. We recalculated monthly mortality rates using the Sablin IMRs and the Watanabe et al. growth rate of 1.16 mm/d producing estimates close to ours, 73.4–94.1% with an average of 86.5%.

The absolute value of total annual production of newly hatched larvae of the Pacific saury can be calculated from our results using the assumptions that 1) all fish in a vertical water column are in the upper one meter, and 2) those in a volume of water strained are captured by the net during the NIT period. The values of larval production at age 0 are on daily basis over the area covered by a net tow. Thus, the annual total production of the hatched larvae can be computed as below:

$$\text{Annual Total Production of Hatched Larvae} = P_0 \cdot 365 \cdot A/401.3$$

where P_0 is larval production at hatching, A is total spawning area in m^2, and 401.3 is surface area in m^2 covered by one net tow. However, the distribution of saury larvae and juveniles in the northwestern Pacific extends far to the east of Japan, and we cannot delimit the total spawning area. Thus, calculation of the absolute larval production of saury at hatching for the entire area is not practical. However, the calculation of abso-

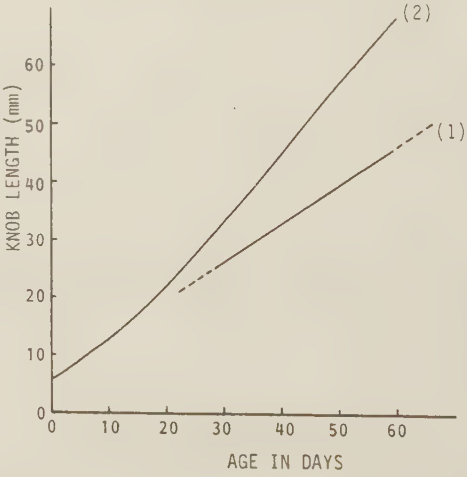

FIGURE 7.—Growth curves used by Sablin (1973) (1) and by us (2) for Pacific saury.

lute larval production in a limited area, which can be covered with a high precision, is possible and will be useful.

The assumption that all the fish in a volume of water strained by the net tow are captured in the NIT period is not realistic for a variety of reasons. The larval net used in this study has bridles in front of the mouth, and to some extent evasion can be expected due to turbulence in front of the net. Visual evasion is possible even in the NIT period because natural waters are not totally dark due to moonlight and a variety of bioluminescent organisms.

Vertical distribution pattern of young sauries has been investigated by towing nets on horizontal strata at several depths (Okiyama 1965; Parin 1967). However, the fraction of the young saury population in the upper one meter available to our net is not known.

The volume of water filtered by a tow may be different among tows depending on wave conditions, mesh clogging, etc. The standardization of catch data by a volume of water filtered must also be done to improve the accuracy of estimates. In our study, we did not have a flow meter with our net. Biases, resulted from these problems, must be resolved before absolute larval production can be obtained.

Unaccounted variances due to the retention correction factor and the duration computed from growth curve could lead to underestimation of the variance of parameter estimates in the mortality curve. On the other hand, the standard error of both P_0 and IMR in the current paper may be higher than the estimates from a regression where each daily fish production estimate is weighted by the inverse of its variance. The effect of the unaccounted variance caused by the retention correction factor could be small because the retention rates were computed from a large number of tows, reducing the standard error of estimated retention to insignificant levels. The variance of duration is unknown. Theoretically it could be estimated from the growth curve, but we did not compute it. A simulation study on evaluating the precision and bias of mortality estimates for northern anchovy (N.C.H.L., unpubl. data) indicated that the variation contributed from bias correction factors is minimal.

We employed an age-independent mortality model in this paper. This does not necessarily mean that the mortality of saury larvae is age-independent. Because of biased catch data due to mesh extrusion in the smallest two size classes, we could not use these two values. This might have had some effect on choosing a mortality model. For further studies we have devised a cylinder-conical larval net for saury that is constructed with one type of mesh (0.53 mm). The body depth at the pectoral fins in early post-yolk-sac larvae is 0.6–0.7 mm, so the new net is expected to retain larvae of the smallest size classes. Thus, the net will enable us to get an unbiased sample of early larvae, and the use of a data set of all size classes including 7.5 and 12.5 mm classes might cause a shift of the mortality model from age-independent to age-dependent type.

Because mortality is a necessary piece of information for computing mean age for each size group, we used the ages corresponding to the midpoints of the size classes for the mortality computation instead of mean ages. It is acceptable to use the midpoint to convert size to age when the mortality information is unavailable, when mortality is low, or when the size interval is small. Bias resulted from the use of the midpoint was large for the first size class: 2.4 days with mortality correction assuming the IMR = 0.08 and 3.2 days using the midpoint 7.7 mm. However, the first two size classes were not included in the mortality computation, so bias caused by using the midpoints was minimal.

The high production values in large juvenile classes (Table 2, Figs. 4, 5) may be due to an underestimation of the durations of these size classes. Year-to-year variations of growth may be large enough to cause considerable differences in durations. The standing stock of larvae in a size class is influenced by the duration of growth through that size class. Because an accurate mortality estimate depends on accurate growth rate estimates, calculation of the growth rate every year, or at least every time the fish size composition changes, is necessary to obtain accurate mortality rates for individual years.

As shown for the northern anchovy, direct estimates of spawning biomass from an ichthyoplankton survey can be obtained (Lasker 1985). This method can be applied to other fishes that produce pelagic eggs. However, the saury produces adhesive eggs and quantitative sampling of them is difficult. Larval census is so far the best index for spawning biomass of the saury. Even if it were possible to obtain quantitative samples of eggs, uncertainties in embryonic mortality rates may rule out use of egg production. The saury has a long incubation time of about 2 weeks under 13°C (Yusa 1960), and slight differences in the daily mortality rates of embryonic stages, rather than egg production, could have profound influence on larval production at hatching. In other words, larval production at hatching may not necessarily be accurately related to egg production without knowing mortality rates of embryonic stages. Although crude estimation of spawning biomass by conventional plankton tows might be possible (Smith et al. 1970), a radical departure from the egg sampling method using information on vertical and horizontal distribution patterns of the eggs is required to devise an egg production method for the saury.

Lo (1985) calculated the time series of egg production at fertilization of the northern anchovy in 1951–82. Year-to-year difference in the egg production was more than 1,000-fold, which is much larger than the difference in saury larval production at hatching in our study, about 33-fold. She also calculated mean yolk-sac larval abundance for the years that showed a difference of more than 1,000-fold. Annual fluctuation of reproductive level in the saury seemed to be smaller than the northern anchovy. This might be related to the differences in spawning ecology of these two species. The saury is reported to be a multiple spawner that spawns in 2 mo intervals in the spawning season (Hatanaka 1955) with a batch fecundity of 500–3,000 egg/female (Hatanaka 1953). The spawning frequency is 3–5 times/yr and the annual fecundity is estimated to be 1,500–15,000. In contrast, time between spawning incidence of the northern anchovy off southern California is 6–8 days and the batch fecundity is 389 eggs/g of ovary free female body weight (Hunter and Goldberg 1980). The saury is less fecund than the northern anchovy and seems to be less variable in its annual fecundity owing to a long maturation period of ovarian eggs. Small year-to-year differences in the reproductive level in the saury might be the result of less variable spawning effort.

The correlation of the larval production at hatching and the daily IMR in the individual years may indicate that the mortality of young saury is density dependent. Watanabe (1987) showed an inverse correlation between the egg abundance and the overall survival rate of larval and juvenile Japanese sardine up to 1 yr old. He further examined correlations between the egg abundance and the biomass of larvae of the 40 mm size class, and between the biomasses of the 40 mm size class and of the 1 yr recruit size class. He found that egg abundance and survival rate up to 40 mm size class are inversely correlated, whereas the biomass of the 40 mm and 1 yr size class are positively correlated. His conclusion was that the mortality rate of larval sardine is density dependent up to 40 mm. Thus, in some pelagic fish, mortality rates of early life stages could be density dependent.

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8979

Larval Fish Diets in Shallow Coastal Waters off San Onofre, California

William Watson and Raymond L. Davis, Jr.

ABSTRACT: Stomach contents were analyzed from the larvae of six common coastal fish taxa (*Atherinopsis californiensis, Leuresthes tenuis, Paralabrax* spp., *Genyonemus lineatus, Seriphus politus*, and *Paralichthys californicus*) collected near San Onofre, California. Samples were collected at night at approximately monthly intervals between September 1978 and September 1979 during a study of ichthyoplankton distributions in these shallow coastal waters.

***Paralabrax* spp. and *Paralichthys californicus* larvae apparently did not feed at night, but high feeding incidences for the atherinids and especially the sciaenids suggested that these larvae did feed during early evening hours. Important components of the diets of all six taxa included the tintinnid genus *Stenosomella*, mollusc veligers, and especially the copepod *Euterpina acutifrons*.**

The vertical distributions of the fish larvae differed from the reported distributions of some of their principal prey taxa, suggesting that factors in addition to, or other than, specific feeding habits are important determinants in the nearshore distributions of fish larvae. The avoidance of seaward dispersal away from the relatively productive and stable nearshore zone may be an important factor influencing larval distribution.

Most studies on the feeding habits of fish larvae in the Southern California Bight have focused on species whose larvae occur primarily beyond the continental shelf, or are broadly distributed across the shelf and beyond (Arthur 1956, 1976; Hunter and Kimbrell 1980; Lasker 1975; Sumida and Moser 1980, 1984; Theilacker 1986). Larval fish feeding in the shallow coastal zone (depth ≤75 m) has, until recently, received relatively little attention. Lasker (1975, 1981) examined the requisite conditions for the successful first feeding of larval northern anchovy and suggested that the shallow nearshore zone may provide a better larval feeding environment than offshore waters, largely because of the more stable nature of the nearshore zone.

It has become increasingly apparent in recent years that this shallow nearshore zone is a unique area supporting distinctive, stable assemblages of fish larvae and zooplankters (Brewer et al. 1981, 1984; Gruber et al. 1982; Barnett et al. 1984; Brewer and Kleppel 1986; Petersen et al. 1986; Barnett and Jahn 1987; Walker et al. 1987). Feeding studies are beginning to be reported for some of the fish larvae that are largely restricted to this zone (Brewer and Kleppel 1986; Jahn et al. 1988).

The purpose of this report is to document the food habits of the larvae of six fish taxa in the shallow coastal waters off southern California. These six taxa include larvae occupying all levels of the water column: larval jacksmelt, *Atherinopsis californiensis*, and grunion, *Leuresthes tenuis*, are largely restricted to the neuston and upper water column; California halibut, *Paralichthys californicus*, and kelp and sand bass, *Paralabrax* spp., larvae occur throughout the water column but tend to be most abundant in midwater; and larval queenfish, *Seriphus politus*, and white croaker, *Genyonemus lineatus*, occur principally in the lower water column and epibenthos (Schlotterbeck and Connally 1982; Barnett et al. 1984; Jahn and Lavenberg 1986). All six taxa occur principally near shore throughout life (Frey 1971; Miller and Lea 1972; Barnett et al. 1984; Lavenberg et al. 1986;).

METHODS

Plankton samples were collected between 25 July 1978 and 23 September 1979 near San Onofre, CA (lat. 33°20′N, long. 117°30′W). The plankton sampling methodology and rationale are detailed by Barnett et al. (1984) and Walker et al. (1987) and are only briefly summarized here.

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Two sample sets, both of which provided complete water column coverage, were utilized in this study. A small sample set, used to make a rough approximation of feeding chronology, consisted of plankton samples collected twice during the day and twice at night within a 24 h period, on two occasions (25 July and 21 September 1978). These samples were collected along the 8 m isobath 1 km south of the San Onofre Nuclear Generating Station (SONGS) (July) and along the 13 m isobath just north of SONGS (September). A larger sample set, used to examine larval diets, consisted of plankton samples collected at night at approximately monthly intervals between 6 September 1978 and 23 September 1979, along a randomly selected isobath within each of five offshore blocks. These blocks were defined by depth contours: (A) 6–9 m, (B) 9–12 m, (C) 12–22 m, (D) 22–45 m, and (E) 45–75 m. The blocks were arrayed between 0.5 and 7.2 km from shore, approximately 1 km south of SONGS.

SONGS Unit 1, a 500 megawatt power plant, operated throughout the study period. Unit 1 has been shown to have had only very localized effects (Marine Review Committee 1979[1]) and it is unlikely to have influenced the results of this study.

Three different types of gear were used to collect both sample sets: a Brown Manta net (Brown and Cheng 1981), to sample the neuston (top 16 cm); a Brown-McGowan opening-closing bongo net, to sample the midwater column; and an Auriga net[2], to sample the epibenthos (within approximately 67 cm of the bottom). All three types of nets were constructed of 0.333 mm mesh Nitex[3], fitted with flowmeters, and towed at ca. 1 m/s to sample a target volume of 400 m^3. All samples were fixed in 10% seawater-formalin.

In the laboratory, the plankton samples were subsampled with a folsom plankton splitter and the fish larvae were sorted from the subsamples at 6–10× magnification under dissecting microscopes. Larvae utilized in the feeding studies were randomly selected from among those sorted from a subsample; a maximum of 100 specimens was selected from any subsample. These larvae were measured to the nearest 0.1 mm notochord or standard length, separated by developmental stage (preflexion = Pr; notochord flexion plus postflexion = FP), placed in a glycerin-water solution, and dissected with fine insect pins. The gut contents of each specimen were identified to the lowest possible taxon using a dissecting (50×) or compound (100–450×) microscope, as appropriate, and enumerated. The number of specimens dissected is listed by species, survey, and sample in Table 1.

Feeding incidence (%FI = percentage of larvae examined that contained at least one food item) was calculated with 95% confidence limits for each larval stage of each taxon. The 95% confidence limits were approximated as $\pm 1.96 (pq/n)^{1/2} + 1/2n$, where p = the proportion containing at least one food item, $q = 1 - p$, and n = the sample size. Percent frequency of occurrence (%FO) and percent of the total number (%N) of prey ingested by each larval fish stage were calculated for each prey type.

RESULTS

Feeding Chronology

Feeding incidence was calculated for *Seriphus politus*, *Paralabrax* spp., and *Paralichthys californicus* which were collected in the day/night sample sets in order to examine feeding chronology (Table 2). Larval *Genyonemus lineatus* and *Atherinopsis californiensis* did not occur in these samples, and too few *Leuresthes tenuis* were available to warrant examination.

During the day, 82% of the *S. politus* larvae contained at least one food item, while at night, 72% contained food. Feeding incidence increased from the morning through the evening, reaching a maximum of 94% for the larvae collected between 2003 and 2101 PST. However, since the feeding incidences were all quite high, and the 95% confidence limits about %FI broadly overlapped for all three morning through evening sampling episodes, it seems likely that there were no real differences in feeding incidence over this period. After midnight, feeding incidence was reduced to 33%, and the 95% confidence limits did not overlap with either the morning or evening values, indicating that feeding incidence indeed was reduced after midnight (Table 2).

Paralabrax spp. feeding incidence was 68%

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[1] Marine Review Committee. 1979. Interim report of the Marine Review Committee to the California Coastal Commission part 1: General summary of findings, predictions, and recommendations concerning the cooling system of the San Onofre Nuclear Generating Station. Mar. Rev. Comm. Doc. 79–02, p. 1–20. Marine Review Committee of the California Coastal Commission, 631 Howard Street, San Francisco, CA 94105.

[2] MBC Applied Environmental Sciences, 947 Newhall Street, Costa Mesa, CA 92627.

[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of fish larvae dissected on each survey date. Pr = preflexion stage larvae; FP = flexion and postflexion stage larvae.

Survey date	*Atherinopsis californiensis*		*Leuresthes tenuis*		*Paralichthys californicus*		*Paralabrax spp.*		*Genyonemus lineatus*		*Seriphus politus*	
	Pr	FP	Pr	FP	Pr	FP	Pr	FP	Pr	FP	Pr	FP
1978												
06 Sept.	0	0	0	24	2	3	30	9	0	0	107	86
02 Oct.	1	0	0	10	15	1	0	0	39	4	13	26
01 Nov.	0	0	0	0	49	1	1	3	17	5	3	2
26 Dec.	2	5	0	0	31	7	0	0	89	33	0	0
1979												
29 Jan.	0	0	0	0	10	0	0	0	138	94	0	0
26 Feb.	2	31	0	0	41	2	0	0	146	98	0	0
26 Mar.	20	21	0	0	0	0	0	0	161	180	23	0
25 Apr.	7	19	7	13	0	0	0	0	40	86	18	0
23 May	0	8	17	20	0	0	0	0	32	49	19	14
25 June	1	1	22	95	0	0	0	0	0	2	51	66
24 July	0	0	0	0	0	0	43	8	0	0	74	14
22 Aug.	0	0	0	9	3	0	13	2	0	0	58	32
20 Sept.	0	0	2	14	35	9	24	2	9	0	87	49
Total	33	85	48	185	186	23	111	24	671	551	453	289

TABLE 2.—Feeding chronology of larval *Paralabrax* spp., *Paralichthys californicus*, and *Seriphus politus*. Survey A samples were collected at the 8 m isobath on 25 July 1978; Survey B samples were collected at the 13 m isobath on 21 September 1978. The time of day when samples were collected is given as Pacific Standard Time. N_t = total number of specimens dissected; N_f = number of specimens containing food; % FI = percent feeding incidence (100 × N_t); 95% confidence limits (C.L.) are given for % FI.

Survey	Time (PST)	*Paralabrax* spp.			*Paralichthys californicus*			*Seriphus politus*		
		N_t	N_f	% FI ± C.L.	N_t	N_f	% FI ± C.L.	N_t	N_f	%FI ± C.L.
A	0547–0626							34	26	76.5 ± 15.7
B	0920–1024	20	11	55.0 ± 24.3	17	9	52.9 ± 26.7			
A	1103–1153							37	32	86.5 ± 12.4
B	1345–1420	14	12	85.7 ± 21.9	7	0	0.0 ± 7.1			
B	1900–1958	18	9	50.0 ± 25.9	26	7	26.9 ± 19.0			
A	2003–2101							70	66	94.3 ± 6.1
B	2354–0049	24	0	0.0 ± 2.1	20	3	15.0 ± 18.1			
A	0118–0150							39	13	33.3 ± 16.1

during the day and 12% at night. Feeding incidence was highest (86%) during midafternoon (1345–1420 PST), dropped to 50% within an hour after sunset, and was 0% by about midnight (Table 2). The 95% confidence limits about %FI were rather broad owing to the small sample sizes, and it is unclear whether there were any real differences in feeding incidence from morning through early evening. However, the large differences in %FI and nonoverlapping confidence limits between the morning through evening and midnight sampling episodes do indicate a real reduction in feeding incidence at night.

Paralichthys californicus larvae displayed a low feeding incidence: 38% during the day and 22% at night. More larvae contained food items during midmorning that at any other time; none contained food in the midafternoon samples (but only seven larvae were available for disssection in the afternoon samples). At night, feeding incidence decreased from 27% about an hour after sunset to 15% by about midnight (Table 2). However, owing to the small sample sizes and consequent broad confidence limits about %FI, it is unclear whether there were any real differences in feeding incidence over this period.

Composition of the Diet

Atherinopsis californiensis

Larval jacksmelt were collected almost exclusively in the neuston in the two sampling blocks (A and B) between the 6 and 12 m isobaths, from October 1978 to June 1979. In total, 118 specimens were dissected (Table 1); 47% of these contained food. The overall feeding inci-

TABLE 3.—Feeding incidence of fish larvae by block, depth stratum, and larval developmental stage. Blocks correspond and E = epibenthos. N_t = total number of larvae dissected; N_f = number of larvae containing food;

Block	Stratum	Number of larvae	*Atherinopsis californiensis*		*Leuresthes tenuis*		*Paralichthys californicus*	
			Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion
A	N	N_t	17	60	11	91	3	4
		N_f	10	31	3	48	2	0
		%FI	58.8 ± 26.3	51.7 ± 13.5	27.3 ± 18.0	52.7 ± 10.8	66.7 ± 70.0	0.0 ± 12.5
	M	N_t	2	1	0	2	5	3
		N_f	2	1	0	1	4	0
		%FI	100.0 ± 25.0	100.0 ± 50.0	—	50.0 ± 94.3	80.0 ± 45.1	0.0 ± 16.7
	E	N_t	0	0	0	0	2	1
		N_f	0	0	0	0	1	0
		%FI	—	—	—	—	50.0 ± 94.3	0.0 ± 50.0
B	N	N_t	11	25	13	31	8	1
		N_f	5	6	10	13	4	0
		%FI	45.5 ± 34.0	24.0 ± 18.7	76.9 ± 26.8	41.9 ± 19.0	50.0 ± 40.9	0.0 ± 50.0
	M	N_t	0	0	0	0	13	0
		N_f	0	0	0	0	2	0
		%FI	—	—	—	—	15.4 ± 23.5	—
	E	N_t	0	0	0	0	2	2
		N_f	0	0	0	0	1	0
		%FI	—	—	—	—	50.0 ± 94.3	0.0 ± 25.0
C	N	N_t	0	2	7	21	10	1
		N_f	0	0	6	3	1	0
		%FI	—	0.0 ± 25.0	85.7 ± 33.1	14.3 ± 17.4	10.0 ± 23.6	0.0 ± 50.0
	M	N_t	0	0	0	0	31	6
		N_f	0	0	0	0	12	2
		%FI	—	—	—	—	38.7 ± 18.8	33.3 ± 46.1
	E	N_t	0	0	0	0	15	0
		N_f	0	0	0	0	5	0
		%FI	—	—	—	—	33.3 ± 27.2	—
D	N	N_t	0	0	8	12	14	0
		N_f	0	0	0	1	4	0
		%FI	—	—	0.0 ± 6.3	8.3 ± 19.8	28.6 ± 27.2	—
	M	N_t	0	0	0	0	47	2
		N_f	0	0	0	0	11	0
		%FI	—	—	—	—	23.4 ± 13.2	0.0 ± 25.0
	E	N_t	0	0	0	0	9	0
		N_f	0	0	0	0	5	0
		%FI	—	—	—	—	55.6 ± 38.0	—
E	N	N_t	0	0	9	28	3	0
		N_f	0	0	0	0	0	0
		%FI	—	—	0.0 ± 5.6	0.0 ± 1.8	0.0 ± 16.7	—
	M	N_t	0	0	0	0	19	3
		N_f	0	0	0	0	3	2
		%FI	—	—	—	—	15.8 ± 19.0	66.7 ± 70.0
	E	N_t	0	0	0	0	4	0
		N_f	0	0	0	0	0	0
		%FI	—	—	—	—	0.0 ± 12.5	—

dence was a little higher for the Pr larvae (56.7 ± 19.4%) than for the older specimens (43.2 ± 10.9%). Both the younger and older larvae displayed a higher feeding incidence in the block nearest shore (Table 3). For the FP larvae summed over all strata, the 95% confidence limits about %FI barely overlapped between block A (52.5 ± 13.4%) and those farther seaward (22.2 ± 17.5%). For the Pr larvae, however, confidence limits broadly overlapped between block

to isobaths: A = 6–9 m; B = 9–12 m; C = 12–22 m; D = 22–45 m; E = 45–75 m. Strata are N = neuston; M = midwater; %FI = feeding incidence (100 × N_f/N_t). Ninety-five percent confidence limits are given for %FI.

Block	Stratum	Number of larvae	*Paralabrax* spp.		*Genyonemus lineatus*		*Seriphus politus*	
			Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion
A	N	N_t	0	3	25	7	2	0
		N_f	0	1	19	7	2	0
		%FI	—	33.3 ± 70.0	76.0 ± 18.7	100.0 ± 7.1	100.0 ± 25.0	—
	M	N_t	0	0	41	11	49	1
		N_f	0	0	35	11	41	1
		%FI	—	—	85.4 ± 12.0	100.0 ± 4.5	83.7 ± 11.4	100.0 ± 50.0
	E	N_t	1	0	53	185	122	153
		N_f	0	0	50	176	98	117
		%FI	0.0 ± 50.0	—	94.3 ± 7.2	95.1 ± 3.4	80.3 ± 7.5	76.5 ± 7.0
B	N	N_t	0	3	26	1	2	0
		N_f	0	0	17	1	1	0
		%FI	—	0.0 ± 16.7	65.4 ± 20.2	100.0 ± 50.0	50.0 ± 94.3	—
	M	N_t	1	0	41	3	44	3
		N_f	0	0	41	3	29	2
		%FI	0.0 ± 50.0	—	100.0 ± 1.2	100.0 ± 16.7	65.9 ± 15.1	66.7 ± 70.0
	E	N_t	2	1	84	168	45	80
		N_f	0	0	83	153	40	62
		%FI	0.0 ± 25.0	0.0 ± 50.0	98.8 ± 2.9	91.1 ± 4.6	88.9 ± 10.3	77.5 ± 9.8
C	N	N_t	3	6	20	1	12	0
		N_f	0	1	16	1	7	0
		%FI	0.0 ± 16.7	16.7 ± 38.2	80.0 ± 20.0	100.0 ± 50.0	58.3 ± 32.0	—
	M	N_t	8	0	34	10	34	9
		N_f	5	0	29	10	23	8
		%FI	62.5 ± 39.8	—	85.3 ± 13.4	100.0 ± 5.0	67.7 ± 17.2	88.9 ± 26.1
	E	N_t	3	1	83	102	18	36
		N_f	1	0	81	102	12	33
		%FI	33.3 ± 70.0	0.0 ± 50.0	97.6 ± 3.9	100.0 ± 0.5	66.7 ± 24.6	91.7 ± 10.4
D	N	N_t	12	0	9	0	29	0
		N_f	0	0	4	0	11	0
		%FI	0.0 ± 4.2	—	44.4 ± 38.0	—	37.9 ± 19.4	—
	M	N_t	57	1	82	13	41	2
		N_f	3	0	79	13	32	2
		%FI	5.3 ± 6.7	0.0 ± 50.0	96.3 ± 4.7	100.0 ± 3.8	78.0 ± 13.9	100.0 ± 25.0
	E	N_t	5	0	128	50	11	5
		N_f	0	0	126	50	7	4
		%FI	0.0 ± 10.0	—	98.4 ± 2.6	100.0 ± 1.0	63.6 ± 33.0	80.0 ± 45.1
E	N	N_t	2	0	11	0	24	0
		N_f	0	0	10	0	12	0
		%FI	0.0 ± 25.0	—	90.9 ± 21.5	—	50.0 ± 22.1	—
	M	N_t	16	6	20	0	20	0
		N_f	7	5	20	0	17	0
		%FI	43.8 ± 27.4	83.3 ± 38.2	100.0 ± 2.5	—	85.0 ± 18.1	—
	E	N_t	1	3	14	0	0	0
		N_f	0	1	13	0	0	0
		%FI	0.0 ± 50.0	33.3 ± 70.0	92.9 ± 17.0	—	—	—

A and those farther seaward. The Pr larvae contained similar average numbers of prey items per feeding individual in blocks A and B (8.8 and 9.2 items per larva, respectively, summed over the water column), but the FP larvae contained nearly twice as many items in block A as in block B (Table 4).

The diet of the jacksmelt larvae varied little with location or over time: except in March 1979, the principal prey for all larval stages was the small harpacticoid copepod *Euterpina acutifrons*. In the March 1979 survey, the Pr larvae fed almost exclusively on *Labidocera trispinosa* nauplii. *Labidocera trispinosa* nauplii also were an appreciable fraction (36%) of the diet of the older jacksmelt larvae on this survey, although *E. acutifrons* still dominated. Minor components of the diet for the Pr larvae included centric diatoms (*Coscinodiscus* spp.), bivalve veligers, tintinnids (*Stenosomella* spp.), cirriped nauplii, and other copepods, e.g., *Paracalanus parvus* (Table 4). The FP larvae consumed all of these items as well, in addition to cirriped cypris larvae and a wider variety of copepods (e.g., *Oncea*, *Oithona*, *Corycaeus*).

Leuresthes tenuis

Larval grunion were collected almost exclusively from the neuston, in all five cross-shelf blocks, in September and Ocotber 1978 and April through September 1979. In total, 233 specimens were dissected (Table 1); 36% contained prey. Overall, feeding incidence differed little between the Pr stage larvae (39.6 ± 14.9%) and older larvae (35.7 ± 7.2%). The FP larvae displayed a

TABLE 4.—Diet of larval *Atherinopsis californiensis*. Results for preflexion stage larvae are given above; those for flexion-postflexion stage larvae are below. A blank column indicates that no larvae containing food occurred in that stratum. Since larval *A. californiensis* occurred only in the blocks A–C neuston and block A midwater, only those strata are shown. Water column strata are N = neuston; M = midwater. %N = the percent of the total food items attributable to a given category; %FO = the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey species include both copepodites and adults.

Block:	A (6–9 m)				B (9–12 m)		C (12–22 m)
Stratum:	N		M		N		N
Prey item	%N	%FO	%N	%FO	%N	%FO	%N
Preflexion							
Coscinodiscus spp.	1.4	10.0	0	0	0	0	
Stenosomella spp.	11.0	30.0	15.2	50.0	0	0	
Bivalve veligers	4.1	20.0	0	0	0	0	
Paracalanus parvus	0	0	3.0	50.0	0	0	
Labidocera trispinosa (nauplii)	52.1	40.0	0	0	97.8	100.0	
Euterpina acutifrons	19.2	50.0	27.3	100.0	2.2	20.0	
E. acutifrons (nauplii)	9.6	30.0	54.5	100.0	0	0	
Cirriped nauplii	2.7	20.0	0	0	0	0	
Total food items	73		33		46		0
Mean prey/feeding larva	7.3		16.5		9.2		0
Flexion-Postflexion							
Coscinodiscus spp.	4.7	6.5	0	0	8.1	16.7	
Stenosomella spp.	4.2	9.7	9.1	100.0	0	0	
Bivalve veligers	1.7	12.9	0	0	0	0	
Paracalanus parvus	0.8	6.5	27.3	100.0	0	0	
Labidocera trispinosa (nauplii)	1.7	3.2	0	0	35.1	33.3	
Oithona oculata	0.3	3.2	0	0	0	0	
Oncea spp.	0	0	0	0	2.7	16.7	
Euterpina acutifrons	79.9	80.6	54.5	100.0	40.5	16.7	
E. acutifrons (nauplii)	5.8	6.5	9.1	100.0	5.4	16.7	
Unidentified copepods	0.8	6.5	0	0	5.4	33.3	
Unidentified	0	0	0	0	2.7	16.7	
Total food items	359		11		37		0
Mean prey/feeding larva	11.6		11.0		6.2		0

clear gradient of feeding incidence from highest nearshore to lowest offshore (Table 3). Feeding incidence for the Pr larvae was highest between about 1 and 3.8 km from shore, and lower both seaward and shoreward, with no overlap of confidence limits (Table 3). Both the Pr and FP larvae consumed more items per feeding individual in the most nearshore block than elsewhere (Table 5). This was especially striking for the Pr larvae.

The most important prey for both the Pr and FP larvae was *Euterpina acutifrons* (Table 5). The Pr larvae tended to utilize *E. acutifrons* nauplii only a little less than the copepodites and adults, while the older larvae showed a clear preference for the copepodites and adults (Table 5). *Coscinodiscus* spp. were important in the diet of the Pr larvae, but constituted only a minor fraction of the FP diet. Minor components of the diet for the Pr larvae included dinoflagellates (*Peridinium* spp.), tintinnids (*Stenosomella* spp.), and small copepods (*Paracalanus parvus* and unidentified nauplii). Older larvae also consumed these items, as well as cirriped nauplii, bivalve veligers, and a wider variety of copepods (e.g., *Oncea*, *Oithona*, *Microsetella*, and *Corycaeus*).

TABLE 5.—Diet of larval *Leuresthes tenuis*. Results for preflexion stage larvae are given above; those for flexion-postflexion stage larvae are below. A blank column indicates that no larvae containing food occurred in that stratum. Since larval *L. tenuis* occurred only in the neuston and midwater, only those strata are shown. Water column strata are N = neuston; M = midwater. %N = the percent of the total food items attributable to a given category; %FO = the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey species include both copepodites and adults.

Block:	A (6–9 m)				B (9–12 m)			C (12–22 m)			D (22–45 m)			E (45–75 m)	
Stratum:	N		M		N		M	N		M	N		M	N	M
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%N	%FO	%N	%N	%FO	%N	%N	%N
Preflexion															
Coscinodiscus spp.	33.3	33.3			0	0		0	0						
Peridinium spp.	3.0	33.3			0	0		0	0						
Stenosomella spp.	6.1	33.3			0	0		0	0						
Euterpina acutifrons	36.4	66.7			17.4	30.0		57.1	66.7						
E. acutifrons (nauplii)	18.1	33.3			0	0		0	0						
Unidentified copepods	3.0	33.3			65.2	80.0		0	0						
Unidentified copepod nauplii	0	0			13.0	10.0		0	0						
Unidentified Crustacea	0	0			0	0		28.6	33.3						
Unidentified	0	0			4.3	10.0		14.3	16.7						
Total food items	33		0		23		0	7		0	0		0	0	0
Mean prey/feeding larva	11.0		0		2.3		0	1.2		0	0		0	0	0
Flexion-postflexion															
Coscinodiscus spp.	1.9	10.0	0	0	0	0		0	0		0	0			
Peridinium spp.	0.1	2.1	0	0	0	0		0	0		0	0			
Stenosomella spp.	2.0	10.0	0	0	0	0		0	0		0	0			
Bivalve Veligers	0.1	2.1	0	0	0	0		0	0		0	0			
Acartia tonsa	0	0	100.0	100.0	0	0		0	0		0	0			
Paracalanus parvus	1.4	10.0	0	0	0.8	7.7		0	0		0	0			
Oithona oculata	0	0	0	0	9.2	15.4		0	0		0	0			
Corycaeus anglicus	0.3	2.1	0	0	0	0		0	0		0	0			
Oncea spp.	1.0	6.3	0	0	0	0		0	0		0	0			
Euterpina acutifrons	62.5	66.7	0	0	82.4	76.9		100.0	100.0		100.0	100.0			
E. acutifrons (nauplii)	15.5	37.5	0	0	0	0		0	0		0	0			
Microsetella rosea	0.1	2.1	0	0	0	0		0	0		0	0			
Unidentified copepods	13.2	20.8	0	0	4.2	38.5		0	0		0	0			
Ciiriped nauplii	0.3	4.2	0	0	0	0		0	0		0	0			
Unidentified	1.6	20.8	0	0	3.4	30.8		0	0		0	0			
Total food items	699		1		119		0	21		0	3		0	0	0
Mean prey/feeding larva	14.6		1.0		9.2		0	7.0		0	3.0		0	0	0

Paralichthys californicus

Two hundred and nine larval California halibut were examined from samples collected between September 1978 and February 1979, and in August and September 1979 (Table 1). Most larvae (89%) were Pr stage. The overall 28% feeding incidence was comparable to the 22% nighttime incidence noted in the day/night sample set. Although the feeding incidence for the Pr larvae was nearly 70% higher than that of the FP larvae (29.5 ± 6.9% vs. 17.4 ± 17.7%), it was well within the 95% confidence limits about the FP value. The Pr larvae displayed a higher feeding incidence in the most nearshore block, but only the confidence limits about the %FI values for the most nearshore and seaward blocks failed to overlap (block A: 70.0 ± 33.4%; block E: 11.5 ± 14.2%). The highest feeding incidence for the FP larvae occurred in the 45–75 m depth block, but all confidence limits broadly overlapped owing to the small sample sizes (Table 3). Among the FP larvae, all four specimens that contained food were collected in midwater. Pr larvae in the nearshore blocks typically contained more prey items per individual than did larvae in the most offshore blocks (Table 6).

Larval California halibut consumed few types of prey. Bivalve veligers, *Euterpina acutifrons* nauplii, the tintinnid genus *Stenosomella*, and unidentified material (including unidentified invertebrate eggs, and setae—presumably from polychaete larvae) accounted for most of the diet of the Pr larvae (Table 6). Young larvae consumed a narrower range of prey types near shore than they did farther seaward. Most of the diet near shore was composed of *Stenosomella* spp., while seaward of the 12 m isobath, *Euterpina acutifrons* nauplii, unidentified material, and bivalve veligers constituted the bulk of the diet. The few FP larvae with gut contents contained only unidentifiable material (Table 6).

Paralabrax spp.

Due to the difficulty and uncertainty in separating larval kelp and sand basses, identification was only to the level of genus. A total of 135 larval *Paralabrax* spp. were examined from samples collected between September and November 1978 and between July and Septem-

TABLE 6.—Diet of larval *Paralichthys californicus*. Results for preflexion stage larvae are given above; those for the column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to listed as prey species include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)					
Stratum:	N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Preflexion												
Rhizosolenia spp.	0	0	0	0	0	0	0	0	0	0	0	0
Peridinium spp.	0	0	0	0	0	0	0	0	0	0	0	0
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0
Stenosomella spp.	90.9	100.0	90.6	25.0	100.0	100.0	77.3	25.0	98.2	50.0	0	0
Bivalve veligers	9.1	50.0	0	0	0	0	0	0	0	0	0	0
Euterpina acutifrons (nauplii)	0	0	0	0	0	0	0	0	1.8	50.0	0	0
Unidentified copepods	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified nauplii	0	0	0	0	0	0	0	0	0	0	100.0	100.0
Unidentified	0	0	9.4	75.0	0	0	22.7	75.0	0	0	0	0
Total food items	11		32		23		22		55		2	
Mean prey/feeding larva	5.5		8.0		23.0		5.5		27.5		2.0	
Flexion-postflexion												
Unidentified												
Total food item	0		0		0		0		0		0	
Mean prey/feeding larva	0		0		0		0		0		0	

ber 1979, mainly in midwater, seaward of the 12 m isobath (Table 1). Most of the larvae were Pr stage (82%). Eighteen percent of the larvae dissected contained food, similar to the 21% nighttime average noted in the day/night comparison. There was no clear cross-shelf pattern in feeding incidence (Table 3), but a vertical pattern may have been suggested by the lower incidence in the neuston (3.4 ± 8.3%) and higher incidences in midwater (22.5 ± 9.2%) and epibenthos (13.3 ± 20.5%). Although the average feeding incidence for the Pr larvae (14.7 ± 1.1%) was less than half that for the FP larvae (33.3 ± 20.9%), it still was contained within the broad confidence bounds about the FP value.

Tintinnids, bivalve veligers, and copepods were among the most important prey for larval *Paralabrax* spp. (Table 7). Unidentified items (including invertebrate eggs and setae—presumably from polychaete larvae) constituted the major dietary component for the Pr larvae. However, tintinnids (*Stenosomella* spp.) and bivalve veligers also were important. The FP larvae tended to consume larger items, especially copepods (e.g., *Acartia tonsa Euterpina acutifrons*, and *Oithona oculata*). Both the Pr and the FP larvae typically contained few prey items (Table 7).

Genyonemus lineatus

A total of 1,222 larval white croaker were examined from samples collected between October 1978 and June 1979, and in September 1979 (Table 1). Fifty-five percent of the larvae were Pr stage. Nearly all of the larvae contained food: feeding incidence was 92.8% (±2.0%) for the Pr larvae and 95.6% (±1.0%) for the FP larvae. Feeding incidence was high in all strata and all cross-shelf blocks (Table 3). For both larval stage categories, feeding incidence in the neuston was distinctly lower (75.0 ± 4.8%) than it was in midwater (94.5 ± 1.6%) and epibenthos (96.2 ± 0.7%). There was little evidence of a cross-shelf gradient in feeding incidence for either stage category (Table 3).

Larval white croaker consumed a wide variety of prey types (Tables 8, 9). Pr larvae tended to eat smaller items, particularly tintinnids, bivalve and gastropod veligers, and small copepods, especially all stages of *Euterpina acutifrons* (Table 8). The FP larvae consumed these

flexion-postflexion stage larvae are below. A blank column indicates that no larvae contained food occurred in that stratum. Water a given food category; %FO = the percent of larvae containing food items that contained prey of the given category. Copepods

Block:	C (12–22 m)						D (22–45 m)						E (45–75 m)			
Stratum:	N		M		E		N		M		E		N	M		E
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%N	%FO	%N
Preflexion																
Rhizosolenia spp.	0	0	1.7	8.3	0	0	0	0	0	0	0	0		0	0	
Peridinium spp.	0	0	1.7	8.3	0	0	0	0	3.3	9.1	0	0		0	0	
Radiolaria	0	0	0	0	0	0	0	0	3.3	9.1	0	0		0	0	
Stenosomella spp.	0	0	5.0	8.3	0	0	0	0	0	0	0	0		0	0	
Bivalve veligers	0	0	1.7	8.3	8.3	20.0	20.0	50.0	16.7	9.1	50.0	20.0		0	0	
Euterpina acutifrons (nauplii)	0	0	78.3	58.3	50.0	80.0	70.0	75.0	36.7	36.4	20.0	20.0		0	0	
Unidentified copepods	0	0	0	0	16.7	20.0	0	0	0	0	0	0		33.3	33.3	
Unidentified nauplii	0	0	0	0	0	0	0	0	0	0	0	0		0	0	
Unidentified	100.0	100.0	11.7	58.3	25.0	40.0	10.0	25.0	40.0	90.9	30.0	60.0		66.7	66.7	
Total food items	1		60		12		10		30		10		0	3		0
Mean prey/feeding larva	1.0		5.0		2.4		2.5		2.7		2.0		0	1.0		0
Flexion-postflexion																
Unidentified			100.0	100.0										100.0	100.0	
Total food item	0		2		0		0		0		0		0	2		0
Mean prey/feeding larva	0		1.0		0		0		0		0		0	1.0		0

TABLE 7.—Diet of larval *Paralabrax* spp. Results for preflexion stage larvae are given above; those for the flexion-postflexion stage larvae are below. A blank column indicates that no larvae contained food in that stratum. Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to a given food category; %FO = the percent of larvae containing food items that contained prey of the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)				B (9–12 m)			C (12–22 m)					
Stratum:	N		M	E	N	M	E	N		M		E	
Prey item	%N	%FO	%N	%N	%N	%N	%N	%N	%FO	%N	%FO	%N	%FO
Preflexion													
Stenosomella spp.										43.8	20.0	0	0
Bivalve veligers										6.3	20.0	0	0
Paracalanus parvus										0	0	0	0
Euterpina acutifrons										12.5	20.0	0	0
E. acutifrons (nauplii)										6.3	20.0	0	0
Unidentified copepods										0	0	0	0
Cirriped nauplii										6.3	20.0	0	0
Unidentified										25.0	80.0	100.0	100.0
Total food items	0	0	0	0	0	0	0	0		16		2	
Mean prey/feeding larva	0	0	0	0	0	0	0	0		3.2		2.0	
Flexion-postflexion													
Acartia tonsa	0	0						100.0	100.0				
Corycaeus anglicus	0	0						0	0				
Oithona oculata	0	0						0	0				
Euterpina acutifrons	0	0						0	0				
Unidentified copepods	0	0						0	0				
Euphausid calyptopis	0	0						0	0				
Unidentified	100.0	100.0						0	0				
Total food items	1	0	0	0	0	0	0	1		0		0	
Mean prey/feeding larva	1.0	0	0	0	0	0	0	1.0		0		0	

Block:	D (22–45 m)				E (45–75 m)				
Stratum:	N	M		E	N	M		E	
Prey item	%N	%N	%FO	%N	%N	%N	%FO	%N	%FO
Preflexion									
Stenosomella spp.		0	0			0	0		
Bivalve veligers		80.0	67.7			9.1	14.3		
Paracalanus parvus		0	0			18.2	14.3		
Euterpina acutifrons		0	0			0	0		
E. acutifrons (nauplii)		0	0			0	0		
Unidentified copepods		20.0	33.3			0	0		
Cirriped nauplii		0	0			0	0		
Unidentified		0	0			72.7	85.7		
Total food items	0	5		0	0	11		0	
Mean prey/feeding larva	0	1.7		0	0	1.6		0	
Flexion-postflexion									
Acartia tonsa						14.3	20.0	0	0
Corycaeus anglicus						0	0	33.3	100.0
Oithona oculata						42.9	20.0	0	0
Euterpina acutifrons						14.3	20.0	33.3	100.0
Unidentified copepods						14.3	20.0	33.3	100.0
Euphausid calyptopis						14.3	20.0	0	0
Unidentified						0	0	0	0
Total food items	0	0		0	0	7		3	
Mean prey/feeding larva	0	0		0	0	1.4		3.0	

small items as well, but in addition consumed larger items such as larger copepod species and mysids (Table 9). Cross-shelf patterns in dietary composition were apparent; for example, tintinnids in the Pr diet shifted from *Stenosomella* spp. near shore to predominantly *Condonaria* spp. farthest from shore (Table 8). Pr larvae also tended to consume more bivalve veligers more frequently in the blocks farthest from shore, but more gastropod veligers nearer shore (Table 8). The FP larvae likewise consumed most gastropod veligers nearer shore, but did not display clear evidence of a cross-shelf pattern in the consumption of bivalve veligers (Table 9). The average number of prey items consumed by the Pr larvae ranged from 2.9 to 8.8 per feeding individual (Table 8), while for the FP larvae the number of items consumed ranged from 2.0 to 8.3 (Table 9). Cross-shelf patterns in the number of items consumed were not apparent. The FP larvae contained more prey items per feeding individual in midwater and epibenthos than in the neuston. There were no consistent differences between strata for the Pr larvae or between midwater and epibenthos samples for the older larvae (Tables 8, 9).

Seriphus politus

A total of 742 larval queenfish (61% Pr stage) were examined from samples collected between September and November 1978 and between March and September 1979 (Table 1). The overall 67% feeding incidence was comparable to the 72% night incidence noted in the day/night sample set. Feeding incidence differed little between the Pr larvae (73.5 ± 4.2%) and the FP larvae (79.2 ± 4.8%). Relatively few larvae were available for dissection from the neuston samples, and overall these larvae displayed the lowest feeding incidence (48.5 ± 12.6% for the Pr larvae; no FP larvae occurred in the neuston). Feeding incidence differed little between midwater (76.4 ± 6.1%) and epibenthos (79.4 ± 3.8%). The feeding incidence for the Pr larvae was highest in block A (81.5 ± 6.1%) where larval abundance was highest, and ranged between about 62 and 68% in the remaining blocks. Confidence limits about the means for blocks B (63.1 ± 9.4%) and D (61.7 ± 11.2%) did not overlap the confidence limits about the mean for block A, but those about the means for blocks C (66.7 ± 12.4%) and E (65.9 ± 15.1%) did overlap the confidence limits about the block A mean. The lowest feeding incidences for the FP larvae occurred in blocks A (76.6 ± 7.0%) and B (77.1 ± 9.6%) where larval abundance was highest, and the highest feeding incidences occurred in blocks C (91.1 ± 9.4%) and D (85.7 ± 33.1%) where larval abundance was low. However, the confidence bounds about these estimates overlapped in all cases.

Larval queenfish consumed a wide variety of prey types (Tables 10, 11). Pr larvae consumed mainly small items, especially bivalve veligers and small copepods such as *Paracalanus parvus* and *Euterpina acutifrons* (Table 10). The FP larvae also consumed these small items in addition to larger items, especially mysids and gammarid amphipods (Table 11). Cross-shelf patterns in dietary composition and number of items consumed were not clear. For the Pr larvae, feeding specimens contained fewer prey items per individual in block E than elsewhere (Table 10), but for the FP larvae no pattern was apparent (Table 11). Both the Pr and FP larvae tended to consume slightly more prey items per feeding individual in midwater than in epibenthos. Smaller prey contributed larger fractions of the diet in midwater than in the epibenthos for both larval stage classes.

DISCUSSION

Both the limited day/night sample series and the much larger night-only sample set indicated that larvae contained food well into the night. A nonzero feeding incidence does not necessarily imply recent feeding, however, but only indicates the presence of food in the gut. For example, a slow digestion and evacuation rate might result in the appearance of nocturnal feeding even if the larvae in fact were not feeding. On the other hand, a low feeding incidence does not necessarily imply nonfeeding, especially for taxa that have a straight gut, since these larvae frequently void their gut contents during capture and fixation (June and Carlson 1971; Hay 1981). Hunter (1981) noted that fish larvae are visual feeders lacking rods and retinomotor pigment migration (e.g., Blaxter 1968) and are probably largely restricted to feeding in daylight hours. The low feeding incidences noted for larval *Paralabrax* spp. in the night samples suggests that they do feed only during the day. Similarly, *Paralichthys californicus* larvae may feed only during the day, although their day-night differences in feeding incidence were smaller and less convincing owing to the broad confidence limits about the %FI values. Both

TABLE 8.—Diet of preflexion stage larvae of *Genyonemus lineatus*. A blank column indicates that no larvae contained food in that stratum. Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to a given food category; %FO = the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey species include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)						C (12–22 m)					
Stratum:	N		M		E		N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	0	0	0	0	0	0	0	0	0.6	2.4	0	0	0	0	0.9	4.9
Peridinium spp.	3.8	10.5	0.7	2.9	0	0	1.3	5.9	2.0	9.8	0.1	1.2	0	0	3.6	10.3	1.1	4.9
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenosomella spp.	37.7	10.5	43.3	25.7	4.4	8.0	21.8	23.5	18.1	24.4	0.6	1.2	0	0	0.7	3.4	0	0
Condonaria spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalve veligers	6.6	26.3	4.6	17.1	3.2	8.0	12.8	35.3	8.3	31.7	7.5	20.5	5.4	6.3	3.6	13.8	9.4	24.7
Gastropod veligers	2.8	15.8	1.3	8.6	0.6	2.0	3.8	17.6	3.1	7.3	1.7	6.0	0	0	1.5	6.9	1.1	6.2
Spionidae	0	0	0	0	0	0	0	0	0	0	0.3	1.2	0	0	0	0	0	0
Polychaete trochophores	0	0	0.3	2.9	5.7	18.0	0	0	0.4	2.4	0.6	2.4	1.8	6.3	1.5	6.9	1.1	6.2
Cyphonautes, uniden.	0	0	0	0	0	0	0	0	0	0	0.6	1.2	0	0	0	0	0.2	1.2
Penilia avirostris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladocerans, uniden.	0	0	0	0	0	0	1.3	5.9	0	0	0	0	0	0	0	0	0	0
Paracalanus parvus	0	0	3.9	17.1	10.1	18.0	0	0	0.4	2.4	1.7	7.2	0	0	0	0	1.1	4.9
Oithona oculata	0	0	1.0	8.6	1.3	4.0	1.3	5.9	0	0	5.8	14.5	0	0	2.2	3.4	2.5	6.2
O. oculata nauplii	0	0	0	0	0	0	0	0	0.4	2.4	1.7	6.0	0	0	2.2	6.9	0.9	4.9
Corycaeus anglicus	0	0	0	0	1.3	4.0	0	0	0.4	2.4	0.9	3.6	0	0	0	0	6.2	16.0
Oncea spp.	0	0	0.3	2.9	0	0	0	0	0	0	0.9	3.6	0	0	1.5	3.4	3.9	4.9
Euterpina acutifrons	16.1	36.8	18.9	60.0	27.8	48.0	17.9	35.3	15.7	61.0	38.9	42.2	5.4	18.8	24.1	44.8	32.5	64.2
E. acutifrons nauplii	6.6	15.8	13.0	28.6	7.6	12.0	15.4	23.5	25.2	39.0	2.9	9.6	46.4	50.0	17.5	34.5	12.1	29.6
Microsetella rosea	0	0	0.3	2.9	0	0	5.1	17.6	3.9	14.6	3.5	8.4	0	0	9.5	20.7	10.5	19.8
M. rosea nauplii	0	0	0	0	0	0	0	0	0.8	4.9	0	0	0	0	0	0	0.2	1.2
Longipedia spp. nauplii	1.9	10.5	0	0	0	0	3.8	11.8	3.1	9.8	0	0	3.6	12.5	2.9	10.3	1.6	8.6
Copepods, unidentified	0	0	0	0	12.7	18.0	0	0	0.8	2.4	5.2	9.6	3.6	6.3	2.9	10.3	1.6	4.9
Copepod nauplii, uniden.	0	0	0	0	0.6	2.0	0	0	0	0	0	0	0	0	0	0	0.5	1.2
Ostracods, uniden.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumaceans, uniden.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausids, calyptopis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	24.5	78.9	12.4	60.0	24.6	46.0	15.4	58.8	17.3	48.8	26.5	55.4	33.9	68.8	26.3	58.6	12.4	44.4
Total food items	106		307		158		78		254		347		56		137		437	
Mean prey/feeding larva	5.6		8.8		3.2		4.6		6.2		4.2		3.5		4.7		5.4	

TABLE 8.—*Continued.*

Block:	D (22–45 m)						E (45–75 m)					
Stratum:	N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	1.0	3.8	0.9	2.4	0	0	0	0	0	0
Peridinium spp.	0	0	8.0	13.9	0.6	2.4	6.9	10.0	6.4	25.0	0	0
Radiolaria	0	0	0.5	1.3	0	0	0	0	0	0	0	0
Stenosomella spp.	0	0	0	0	0	0	0	0	3.8	5.0	3.6	7.7
Condonaria spp.	0	0	1.5	5.1	0	0	24.1	30.0	5.1	20.0	0	0
Bivalve veligers	22.7	25.0	40.5	62.0	19.4	35.7	24.1	50.0	19.2	60.0	16.4	38.5
Gastropod veligers	0	0	0.8	3.8	1.2	5.6	0	0	0	0	0	0
Spionidae	0	0	0	0	0	0	0	0	0	0	0	0
Polychaete trochophores	0	0	0	0	0.6	3.2	0	0	2.6	10.0	1.8	7.7
Cyphonautes, uniden.	0	0	0.5	2.5	0.5	1.6	0	0	0	0	0	0
Penilia avirostris	0	0	0	0	0.2	0.8	0	0	0	0	0	0
Cladocerans, uniden.	0	0	0	0	0	0	0	0	0	0	0	0
Paracalanus parvus	0	0	0	0	0.5	2.4	0	0	0	0	0	0
Oithona oculata	0	0	0	0	2.9	9.5	0	0	0	0	0	0
O. oculata nauplii	4.5	25.0	1.5	7.6	0	0	0	0	0	0	0	0
Corycaeus anglicus	0	0	0.5	2.5	1.7	5.6	0	0	0	0	0	0
Oncea spp.	0	0	1.5	5.1	0.8	3.2	0	0	3.8	10.0	3.6	15.4
Euterpina acutifrons	4.5	25.0	21.6	39.2	57.9	80.2	0	0	0	0	1.8	7.7
E. acutifrons nauplii	13.6	50.0	10.3	22.8	1.2	4.0	3.4	10.0	5.1	10.0	0	0
Microsetella rosea	13.6	25.0	5.0	16.5	3.5	9.5	0	0	2.6	10.0	0	0
M. rosea nauplii	0	0	0	0	0	0	13.8	40.0	2.6	10.0	5.5	15.4
Longipedia spp. nauplii	22.7	25.0	0	0	0	0	3.4	10.0	0	0	0	0
Copepods, unidentified	0	0	0	0	0.6	2.4	0	0	1.3	5.0	0	0
Copepod nauplii, uniden.	0	0	0.5	1.3	0	0	3.4	10.0	1.3	5.0	0	0
Ostracods, uniden.	0	0	0	0	0.2	0.8	0	0	0	0	1.8	7.7
Cumaceans, uniden.	0	0	0	0	0.2	0.8	0	0	0	0	0	0
Euphausids, calyptopis	0	0	0	0	0.5	2.4	0	0	0	0	0	0
Unidentified	18.2	50.0	6.3	15.2	6.6	23.8	20.7	60.0	46.2	65.0	65.5	61.5
Total food items	22		398		648		29		78		55	
Mean prey/feeding larva	5.5		5.0		5.1		2.9		3.9		4.2	

TABLE 9.—Diet of flexion-postflexion stage larvae of *Genyonemus lineatus*. Since none of these larvae occurred in block Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)					
Stratum:	N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	0	0	0.2	0.6	0	0	6.3	33.3	0	0
Rhizosolenia spp.	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Peridinium spp.	0	0	0	0	0	0	0	0	0	0	0	0
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta spp.	0	0	0	0	0.4	1.1	0	0	0	0	0.2	1.3
Bivalve veligers	6.3	14.3	9.1	63.6	2.3	7.4	0	0	0	0	5.8	19.0
Gastropod veligers	12.5	28.6	1.3	9.1	0.5	2.3	0	0	0	0	1.9	5.2
Spionidae	6.3	14.3	1.3	9.1	0.5	2.3	0	0	0	0	0	0
Polychaete larvae	0	0	9.1	27.3	2.3	5.7	0	0	6.3	33.3	9.5	26.1
Membranipora spp. cyphonautes	0	0	0	0	0.1	0.6	0	0	0	0	0.1	0.7
Cyphonautes, uniden.	0	0	0	0	0.8	4.0	0	0	0	0	1.0	3.9
Penilia avirostris	0	0	0	0	0.2	1.1	0	0	0	0	0	0
Acartia tonsa	0	0	0	0	0.1	0.6	0	0	0	0	2.1	9.8
Paracalanus parvus	37.5	28.6	32.5	63.6	54.1	48.9	0	0	18.8	66.7	29.5	51.0
Labidocera trispinosa	0	0	1.3	9.1	4.5	9.7	0	0	12.5	33.3	1.2	4.6
Pontellopsis spp.	0	0	0	0	0	0	0	0	0	0	2.6	7.8
Candacia spp.	0	0	0	0	0	0	0	0	0	0	0	0
Oithona oculata	0	0	3.9	27.3	1.1	3.4	0	0	0	0	0.6	2.6
O. oculata nauplii	0	0	0	0	0	0	0	0	0	0	0	0
O. plumifera	0	0	0	0	0	0	0	0	0	0	0.2	1.3
Corycaeus anglicus	0	0	2.6	9.1	0.6	2.3	0	0	0	0	1.1	5.9
Oncea spp.	0	0	0	0	0.2	1.1	0	0	0	0	0.3	2.0
Euterpina acutifrons	18.8	42.9	31.2	81.8	12.0	30.1	0	0	50.0	100.0	30.3	54.2
E. acutifrons nauplii	6.3	14.3	0	0	1.7	6.3	0	0	0	0	0.2	1.3
Microsetella rosea	0	0	0	0	0.1	0.6	0	0	0	0	0.3	2.0
Longipedia spp. nauplii	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Copepods, uniden.	0	0	0	0	11.3	32.4	0	0	0	0	4.3	14.4
Copepod nauplii, uniden.	6.3	14.3	1.3	9.1	0	0	0	0	0	0	0	0
Cirriped nauplii	0	0	0	0	0.1	0.6	0	0	0	0	0.5	2.0
Cirriped cypris	0	0	0	0	0.1	0.6	0	0	0	0	0.2	1.3
Nebalia spp.	0	0	1.3	9.1	0	0	0	0	0	0	0.1	0.7
Ostracods, uniden.	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Metamysidopsis elongata	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Mysidopsis californica	0	0	0	0	0	0	0	0	0	0	0.3	2.0
M. intii	0	0	0	0	0	0	0	0	0	0	0.2	0.7
Neomysis rayii	0	0	0	0	0	0	0	0	0	0	0.3	2.0
Neomysis spp. juveniles	0	0	0	0	1.4	5.1	0	0	0	0	0.3	1.3
Siriella pacifica	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Mysids, uniden.	0	0	0	0	0.8	2.3	0	0	0	0	0.7	3.9
Gammarids, uniden.	0	0	0	0	1.4	5.7	0	0	0	0	0.3	2.0
Euphausids, calyptopis	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Caridean zoeae	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Brachyuran zoeae	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Brachyuran megalopae	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Fish larvae	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	6.3	14.3	5.2	27.3	2.6	9.1	100.0	100.0	6.3	33.3	5.0	24.8
Total food items	16		77		844		2		16		884	
Mean prey/feeding larva	2.3		7.0		4.8		2.0		5.3		5.8	

E, that block is not included on the table. A blank column indicates that no larvae contained food in that stratum. attributable to a given food category; %FO = the percent of the larvae containing food items that contained prey of

Block:	C (22–45 m)						D (45–75 m)				
Stratum:	N		M		E		N	M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	0	0	0.5	2.9		0	0	0.6	4.0
Rhizosolenia spp.	0	0	0	0	0	0		0	0	0	0
Peridinium spp.	0	0	0	0	0.6	2.0		0	0	0.3	2.0
Radiolaria	0	0	0	0	0.1	1.0		0	0	0	0
Sagitta spp.	0	0	0	0	0	0		0	0	0.3	2.0
Bivalve veligers	0	0	7.4	30.0	2.1	12.7		6.2	23.1	4.5	22.0
Gastropod veligers	0	0	3.7	20.0	1.2	9.8		0	0	2.9	18.0
Spionidae	0	0	0	0	0	0		0	0	0.3	2.0
Polychaete larvae	0	0	0	0	6.1	25.5		0	0	0.3	2.0
Membranipora spp. cyphonautes	0	0	0	0	0	0		0	0	0	0
Cyphonautes, uniden.	0	0	0	0	0.5	2.0		0	0	0.3	2.0
Penilia avirostris	0	0	0	0	0	0		0	0	0	0
Acartia tonsa	0	0	0	0	0	0		0	0	0	0
Paracalanus parvus	0	0	7.4	30.0	18.0	37.3		0	0	1.9	6.0
Labidocera trispinosa	0	0	0	0	0	0		0	0	0	0
Pontellopsis spp.	0	0	0	0	4.0	18.6		0	0	0	0
Candacia spp.	0	0	1.9	10.0	0	0		0	0	0	0
Oithona oculata	0	0	9.3	10.0	0.7	5.9		4.9	7.7	4.2	10.0
O. oculata nauplii	0	0	0	0	0.2	2.0		1.2	7.7	0	0
O. plumifera	0	0	1.9	10.0	0	0		0	0	0	0
Corycaeus anglicus	0	0	1.9	10.0	6.3	28.4		1.2	7.7	4.2	16.0
Oncea spp.	0	0	27.8	50.0	15.2	33.3		2.5	7.7	1.0	4.0
Euterpina acutifrons	33.3	100.0	29.6	40.0	31.4	61.8		65.4	92.3	70.2	86.0
E. acutifrons nauplii	0	0	0	0	0	0		9.9	15.4	0.3	2.0
Microsetella rosea	0	0	3.7	20.0	2.4	12.7		1.2	7.7	1.6	8.0
Longipedia spp. nauplii	0	0	0	0	0	0		0	0	0	0
Copepods, uniden.	66.7	100.0	0	0	1.3	4.9		0	0	2.9	10.0
Copepod nauplii, uniden.	0	0	0	0	3.8	2.0		0	0	0	0
Cirriped nauplii	0	0	0	0	0	0		0	0	0	0
Cirriped cypris	0	0	0	0	0	0		0	0	0	0
Nebalia spp.	0	0	0	0	0	0	0	0	0	0	0
Ostracods, uniden.	0	0	0	0	0	0	0	0	0	0.3	2.0
Metamysidopsis elongata	0	0	0	0	0	0	0	0	0	0	0
Mysidopsis californica	0	0	0	0	0	0		0	0	0	0
M. intii	0	0	0	0	0	0		0	0	0	0
Neomysis rayii	0	0	0	0	0.5	3.9		0	0	1.0	6.0
Neomysis spp. juveniles	0	0	0	0	0	0		0	0	0	0
Siriella pacifica	0	0	0	0	0	0		0	0	0	0
Mysids, uniden.	0	0	0	0	0	0		0	0	0	0
Gammarids, uniden.	0	0	0	0	0	0		0	0	0	0
Euphausids, calyptopis	0	0	0	0	0.2	2.0		1.2	7.7	0	0
Caridean zoeae	0	0	0	0	0.2	2.0		0	0	0	0
Brachyuran zoeae	0	0	0	0	0.1	1.0		0	0	0	0
Brachyuran megalopae	0	0	0	0	0	0		0	0	0	0
Fish larvae	0	0	0	0	0.1	1.0		0	0	0	0
Unidentified	0	0	5.6	20.0	4.0	25.5		6.2	23.1	2.6	14.0
Total food items	3		54		846		0	81		309	
Mean prey/feeding larva	3.0		5.4		8.3		0	6.2		6.2	

TABLE 10.—Diet of preflexion stage larvae of *Seriphus politus*. A blank column indicates that no larvae contained food in that stratum. Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to a given food category; %FO the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)						C (12–22 m)					
Stratum:	N		M		E		N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenosomella spp.	0	0	0	0	0	0	0	0	20.0	10.3	0	0	20.5	14.3	12.3	13.0	0	0
Condonaria spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tintinnids, uniden.	0	0	4.2	7.3	0	0	0	0	1.4	3.4	0	0	0	0	0	0	0	0
Bivalve veligers	7.7	50.0	7.1	19.5	3.0	8.2	0	0	2.9	3.4	1.5	7.5	7.7	28.6	8.6	30.4	4.8	16.7
Gastropod veligers	0	0	1.8	7.3	1.7	4.1	0	0	1.4	3.4	0.5	2.5	0	0	0	0	2.4	8.3
Polychaete larvae	0	0	0	0	0	0	0	0	1.4	3.4	0	0	0	0	0	0	0	0
Evadne nordmanni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acartia tonsa	0	0	0	0	0.3	1.0	0	0	0	0	0	0	0	0	2.5	8.7	0	0
Paracalanus parvus	0	0	6.5	22.0	17.2	31.6	0	0	4.3	10.3	5.4	25.0	0	0	0	0	2.4	8.3
Oithona oculata	0	0	5.4	4.9	8.9	14.3	0	0	5.7	3.4	1.5	7.5	2.6	14.3	22.2	17.4	0	0
O. plumifera	0	0	0	0	0	0	0	0	0	0	0.5	2.5	0	0	0	0	2.4	8.3
Corycaeus anglicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.4	8.3
Euterpina acutifrons	0	0	56.0	75.6	46.8	55.1	0	0	41.4	69.0	69.8	82.5	5.1	14.3	6.2	21.7	45.2	33.3
E. acutifrons nauplii	69.2	50.0	4.8	14.6	0.6	2.0	0	0	2.9	6.9	0.5	2.5	41.0	28.6	21.0	21.7	11.9	33.3
Microsetella rosea	0	0	0	0	0	0	0	0	0	0	1.0	5.0	0	0	0	0	0	0
M. rosea nauplii	0	0	0	0	0	0	0	0	0	0	0	0	2.6	14.3	0	0	0	0
Copepods, uniden.	0	0	1.8	7.3	10.0	23.5	0	0	7.1	13.8	3.9	17.5	5.1	28.6	7.4	21.7	7.1	16.7
Copepod nauplii, uniden.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5	8.7	0	0
Longipedia spp. nauplii	15.4	100.0	1.8	7.3	0	0	0	0	0	0	0	0	0	0	4.9	8.7	0	0
Holmesimysis costata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.4	8.3
Neomysis spp., juveniles	0	0	0	0	0.3	1.0	0	0	0	0	0	0	0	0	0	0	0	0
Mysids, uniden.	0	0	0	0	0.6	2.0	0	0	0	0	0.5	2.5	0	0	0	0	0	0
Cumaceans, uniden.	0	0	0	0	0	0	0	0	0	0	0.5	2.5	0	0	0	0	2.4	8.3
Gammarids, uniden.	0	0	0	0	0.8	3.1	0	0	0	0	0	0	0	0	0	0	7.1	16.7
Crustaceans, uniden.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	7.7	50.0	10.7	43.9	10.0	35.7	100.0	100.0	11.4	27.6	14.6	75.0	15.4	57.1	12.3	43.5	9.5	33.3
Total food items	13		168		361		1		70		205		39		81		42	
Mean prey/feeding larva	6.5		4.1		3.7		1.0		2.4		5.1		5.6		3.5		3.5	

TABLE 10.—*Continued.*

Block:	D (22–45 m)						E (45–75 m)				
Stratum:	N		M		E		N		M		E
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%F	%N
Radiolaria	0	0	0	0	0	0	0	0	3.0	5.9	
Stenosomella spp.	0	0	14.2	18.8	0	0	42.9	16.7	12.1	11.8	
Condonaria spp.	0	0	1.5	6.3	0	0	0	0	0	0	
Tintinnids, uniden.	0	0	0	0	0	0	0	0	0	0	
Bivalve veligers	12.1	18.2	25.4	37.5	0	0	0	0	27.3	29.4	
Gastropod veligers	0	0	0.7	3.1	0	0	0	0	0	0	
Polychaete larvae	3.0	9.1	0	0	0	0	0	0	0	0	
Evadne nordmanni	0	0	0.7	3.1	0	0	0	0	0	0	
Acartia tonsa	0	0	0.7	3.1	0	0	0	0	0	0	
Paracalanus parvus	12.1	18.2	1.5	6.3	0	0	0	0	0	0	
Oithona oculata	0	0	20.9	21.9	5.9	14.3	0	0	3.0	5.9	
O. plumifera	0	0	0	0	0	0	0	0	0	0	
Corycaeus anglicus	0	0	0	0	0	0	0	0	0	0	
Euterpina acutifrons	27.3	18.2	5.2	18.8	5.9	14.3	4.8	8.3	0	0	
E. acutifrons nauplii	0	0	1.5	6.3	5.9	14.3	0	0	3.0	5.9	
Microsetella rosea	0	0	0	0	0	0	0	0	0	0	
M. rosea nauplii	0	0	0	0	0	0	0	0	0	0	
Copepods, uniden.	18.2	36.4	5.2	18.8	41.2	42.9	0	0	0	0	
Copepod nauplii, uniden.	3.0	9.1	0	0	17.6	14.3	0	0	6.1	11.8	
Longipedia spp. nauplii	0	0	0	0	0	0	0	0	0	0	
Holmesimysis costata	0	0	0	0	0	0	0	0	0	0	
Neomysis spp., juveniles	0	0	0	0	0	0	0	0	0	0	
Mysids, uniden.	0	0	0.7	3.1	0	0	0	0	0	0	
Cumaceans, uniden.	0	0	0	0	0	0	0	0	0	0	
Gammarids, uniden.	0	0	0	0	0	0	0	0	0	0	
Crustaceans, uniden.	0	0	0	0	0	0	4.8	8.3	0	0	
Unidentified	24.2	54.5	21.6	40.6	23.5	57.1	47.6	83.3	45.5	54.7	
Total food items	33		134		17		21		33		0
Mean prey/feeding larva	3.0		4.2		2.4		1.8		1.9		0

TABLE 11.—Diet of flexion-postflexion stage larvae of *Seriphus politus*. A blank column indicates that no column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items prey of the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)					B (9–12 m)				
Stratum:	N	M		E		N	M		E	
Prey item	%N	%N	%FO	%N	%FO	%N	%N	%FO	%N	%FO
Sagitta spp.		0	0	0.5	0.9		0	0	0.6	1.6
Bivalve veligers		0	0	0.5	0.9		0	0	0	0
Gastropod veligers		0	0	0	0		0	0	0.6	1.6
Polychaete larvae		0	0	2.6	4.3		0	0	3.1	8.1
Cyphonautes, uniden.		0	0	0	0		0	0	0	0
Evadne nordmanni		0	0	0	0		20.0	50.0	0	0
Acartia tonsa		0	0	8.3	8.5		0	0	3.7	9.7
Paracalanus parvus		0	0	1.6	2.6		0	0	12.3	14.5
Labidocera trispinosa		0	0	0	0		0	0	0.6	1.6
Pontellopsis spp.		0	0	3.6	4.3		0	0	0	0
Oithona oculata		50.0	100.0	1.0	1.7		0	0	0	0
Corycaeus anglicus		0	0	0.5	0.9		0	0	0	0
Oncea spp.		0	0	1.0	0.9		0	0	0	0
Euterpina acutifons		0	0	14.6	13.7		20.0	50.0	32.5	25.8
Microsetella rosea		0	0	0.5	0.9		0	0	0	0
Copepods, uniden.		0	0	9.4	9.4		60.0	100.0	9.8	11.3
Cirriped nauplii		0	0	0	0		0	0	0.6	1.6
Holmesimysis costata		0	0	4.2	6.0		0	0	0.6	1.6
Metamysidopsis elongata		0	0	2.6	3.4		0	0	0	0
Neomysis rayii		0	0	4.2	6.8		0	0	4.9	12.9
Siriella pacifica		0	0	0	0		0	0	1.2	1.6
Mysids, uniden.		12.5	100.0	14.6	19.7		0	0	11.7	25.8
Gammarids, uniden.		12.5	100.0	18.2	22.2		0	0	5.5	14.5
Caridean zoeae		0	0	3.1	5.1		0	0	0.6	1.6
Callianassa spp. zoeae		0	0	0	0		0	0	1.2	3.2
Crustaceans, uniden.		0	0	2.6	4.3		0	0	0.6	1.6
Unidentified		25.0	100.0	6.3	10.3		0	0	9.8	24.2
Total food items	0	8		192		0	5		163	
Mean prey/feeding larva	0	8.0		1.6		0	2.5		2.6	

taxa develop a coil in the gut during the preflexion stage, reducing the likelihood that the low night feeding incidences reflected voiding of the gut contents during capture. The *Paralabrax* spp. feeding incidence was relatively high in the day samples, further suggesting that voiding of the gut contents did not contribute appreciably to the low feeding incidence observed at night.

The higher night feeding incidences for the remaining species, especially *Genyonemus lineatus* and *Seriphus politus*, suggest that they may have continued to feed after dark, at least during the early evening hours. Bagarinao and Hunter (1983) noted that older (≥10 mm) *Engraulis mordax* larvae feed in the dark if prey densities are high enough, and suggested that the full moon provides sufficient illumination for these larvae to feed near the surface at lower prey densities. Other reports of apparent larval fish feeding at night include, for example, Brewer and Kleppel's (1986) report of high feeding incidence until midnight for larval *G. lineatus* collected near shore in Santa Monica Bay, and the reports of Sumida and Moser (1980) and Jenkins (1987) that larval *Merluccius productus* off southern California and *Rhombosolea tapirina* in Port Phillip Bay, Australia, respectively, had high feeding incidences throughout much of the day and night. Brewer and Kleppel (1986) and Sumida and Moser (1980) attributed the high night feeding incidences in their studies to slow digestion rather than to nocturnal feeding, and this cannot be discounted as an alternative explanation for the high nocturnal feeding incidences noted in the present study. This alternative interpretation may be supported by the observation that feeding incidences tended to be lower during the August and September 1979

larvae contained food in that stratum. Block E is not shown because no larvae occurred there. Water
attributable to a given food category; %FO = the percent of the larvae containing food items that contained

Block:	C (12–22 m)					D (22–45 m)				
Stratum:	N	M		E		N	M		E	
Prey item	%N	%N	%FO	%N	%FO	%N	%N	%FO	%N	%FO
Sagitta spp.		0	0	0	0		0	0	0	0
Bivalve veligers		0	0	0	0		0	0	0	0
Gastropod veligers		0	0	0	0		0	0	0	0
Polychaete larvae		0	0	0	0		0	0	0	0
Cyphonautes, uniden.		0	0	1.9	3.0		0	0	0	0
Evadne nordmanni		0	0	0	0		0	0	0	0
Acartia tonsa		52.6	50.0	11.1	12.1		0	0	0	0
Paracalanus parvus		0	0	1.9	3.0		0	0	0	0
Labidocera trispinosa		0	0	7.4	9.0		0	0	0	0
Pontellopsis spp.		0	0	1.9	3.0		0	0	0	0
Oithona oculata		0	0	0	0		0	0	0	0
Corycaeus anglicus		0	0	3.7	6.0		0	0	0	0
Oncea spp.		0	0	0	0		0	0	0	0
Euterpina acutifons		0	0	5.6	9.0		0	0	0	0
Microsetella rosea		0	0	0	0		0	0	0	0
Copepods, uniden.		15.8	25.0	5.6	6.0		100.0	100.0	0	0
Cirriped nauplii		0	0	0	0		0	0	0	0
Holmesimysis costata		0	0	5.6	9.0		0	0	0	0
Metamysidopsis elongata		0	0	1.9	3.0		0	0	0	0
Neomysis rayii		0	0	1.9	3.0		0	0	0	0
Siriella pacifica		0	0	0	0		0	0	0	0
Mysids, uniden.		15.8	37.5	13.0	21.2		0	0	25.0	25.0
Gammarids, uniden.		15.8	25.0	27.8	24.2		0	0	25.0	25.0
Caridean zoeae		0	0	0	0		0	0	0	0
Callianassa spp. zoeae		0	0	0	0		0	0	0	0
Crustaceans, uniden.		0	0	0	0		0	0	0	0
Unidentified		0	0	11.1	18.2		0	0	50.0	50.0
Total food items	0	19		54		0	6		4	
Mean prey/feeding larva	0	2.4		1.6		0	3.0		1.0	

surveys. In both cases, sampling was mainly after midnight, in contrast to all other surveys when sampling was mainly before midnight. The potential influence of moonlight on feeding incidence could not be addressed in this study, since all samples were collected within five days of new moon. However, as noted above, the study by Bagarinao and Hunter (1983) suggests that nocturnal feeding is possible during full moon, at least near the surface.

Cross-shelf differences in feeding incidence were apparent for 5 of the 12 stage-taxon categories examined; for 4 of these, feeding incidence was higher near shore and lower in seaward blocks. This may reflect a higher level of feeding intensity near shore, but since the nearshore blocks were always sampled earlier than the offshore blocks during each survey, the alternative explanation that these patterns merely reflected the cessation of larval feeding at night cannot be dismissed. The results for *Atherinopsis californiensis*, and perhaps for *Leuresthes tenuis*, are more likely to represent real, but small-scale differences in feeding incidence since these two species were collected mainly in the two or three shallowest blocks, and relatively little time elapsed between samples.

The composition of the larval diets described in this study is similar to the diet described for many larval marine teleosts (e.g., Arthur 1976; Sumida and Moser 1980; Hunter 1981) in that major fractions were contributed by copepod nauplii and copepodites. In the present study, the harpacticoid copepod *Euterpina acutifrons* was an important component of the diets of all six taxa examined. This copepod species has not been noted in other studies as being such an important dietary component and the reason for its importance at San Onofre is unknown. *Euterpina acutifrons* may be more abundant near San Onofre than elsewhere (mean density 10,640/m^3—range 1,078–37,314/m^3—between the 9 and 100 m isobaths during a microzooplankton study conducted at San Onofre during the year prior to the feeding study), or it might have been unusually abundant during the year when the feeding studies were done, but appropriate data from long-term and larger scale studies that would allow evaluation of these suggestions are unavailable. Other particularly important copepods were the cyclopoid *Oithona oculata* and the calanoid *Labidocera trispinosa*. However, copepods were not the only important food items in the nearshore zone and were not the dominant prey for some of the Pr stage larvae. Other consistently important prey included tintinnids, especially *Stenosomella* spp., and mollusc veligers (principally bivalves, but also gastropods in some cases). Older sciaenid larvae consumed appreciable numbers of mysids. The diets of the older larvae did not exclude small items such as mollusc veligers or copepod nauplii; instead, the small items continued to be consumed, and larger items such as larger copepod species (e.g., Barnett and Jahn 1987: table 3) were added as well. This is consistent with Hunter's (1981) observation that although the maximum prey size selected increases more or less rapidly with increasing larval fish size, the minimum prey size increases very slowly. Thus larger larvae can select from among a wider range of prey sizes, consuming the energetically more valuable larger items when those are available, and perhaps maintaining on smaller items when large prey are unavailable (Hunter 1976; Hunter and Kimbrell 1980).

Concurrent plankton sampling that would allow comparisons of the spatial distributions of the fish larvae and their prey species was not part of the present study. However, other studies did examine the distribution and abundance of the zooplankton during the day in the same area from 1977 through 1980 (Barnett and Jahn 1987), and spatial patterns of the fish larvae and their prey can be compared in a general way on the basis of these studies. The majority of the most important prey categories occurred in highest concentrations near shore (e.g., Barnett and Jahn 1987). For example, *Oithona oculata* was most abundant in the epibenthos shoreward of the 13 m isobath (Barnett and Jahn 1987), while *Paracalanus parvus* was abundant throughout the water column shoreward of the 30 m isobath (Fig. 1). The Marine Review Committee's unpublished count data, from samples collected at San Onofre on 31 October 1978 indicated that *Euterpina acutifrons* nauplii were approximately 4–34 times more abundant in samples taken at the 9, 13, and 30 m isobaths than in samples from the 100 m isobath (maximum abundance 141,200/m^3, averaged over the water column at 13 m), while the copepodites and adults were 1.5–19 times more abundant at the shallow stations than at the 100 m station (maximum abundance 11,600/m^3, averaged over the water column at 13 m). *Labidocera trispinosa* nauplii were restricted to the very nearshore zone, shoreward of the 13 m isobath, where they occurred throughout the water column (Fig. 1). Bivalve veligers were abundant throughout the water column between the 13 and 30 m isobaths, while gastropod veligers occurred throughout the nearshore zone and seaward to at least the 100 m isobath (Fig. 1). The most frequently occurring mysid taxa in the larval diets—*Holmesimysis costata*, *Neomysis rayii*, and *Neomysis* spp. juveniles—all were most abundant in the epibenthos shoreward of the 15 m isobath (Bernstein and Gleye 1981[4]). Clutter (1967) reported that *H. costata*, as well as several other mysid species, was restricted to the nearshore zone off La Jolla, CA.

Barnett et al. (1984) described the cross-shelf and vertical distributions of the larvae of five of the six fish taxa considered here. All five were most abundant shoreward of the 45 m isobath; larvae of the sixth taxon, *Paralabrax* spp., occur principally shoreward of the 36 m isobath (Lavenberg et al. 1986). The atherinid larvae are almost exclusively neustonic; *Paralichthys californicus* and the *Paralabrax* spp. larvae occur throughout the water column (especially in midwater); and the *Genyonemus lineatus* and *Seriphus politus* larvae are located mainly in the lower water column and epibenthos (Schlotterbeck and Connally 1982; Barnett et al. 1984; Jahn and Lavenberg 1986). Ontogenetic redistributions occur during the larval phase for at least some of the taxa: the flexion and postflexion stage larvae of *G. lineatus* and *S. politus* are more nearshore and epibenthic than the preflexion stage larvae (Barnett et al. 1984), while the transforming postflexion larvae of *Paralichthys californicus* occur most frequently and in

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[4] Bernstein, B. B. and L. G. Gleye. 1981. The ecology of mysids in the San Onofre region. Volume II: New reports. Rep. Mar. Rev. Comm., Rep. No. MEC01281999.

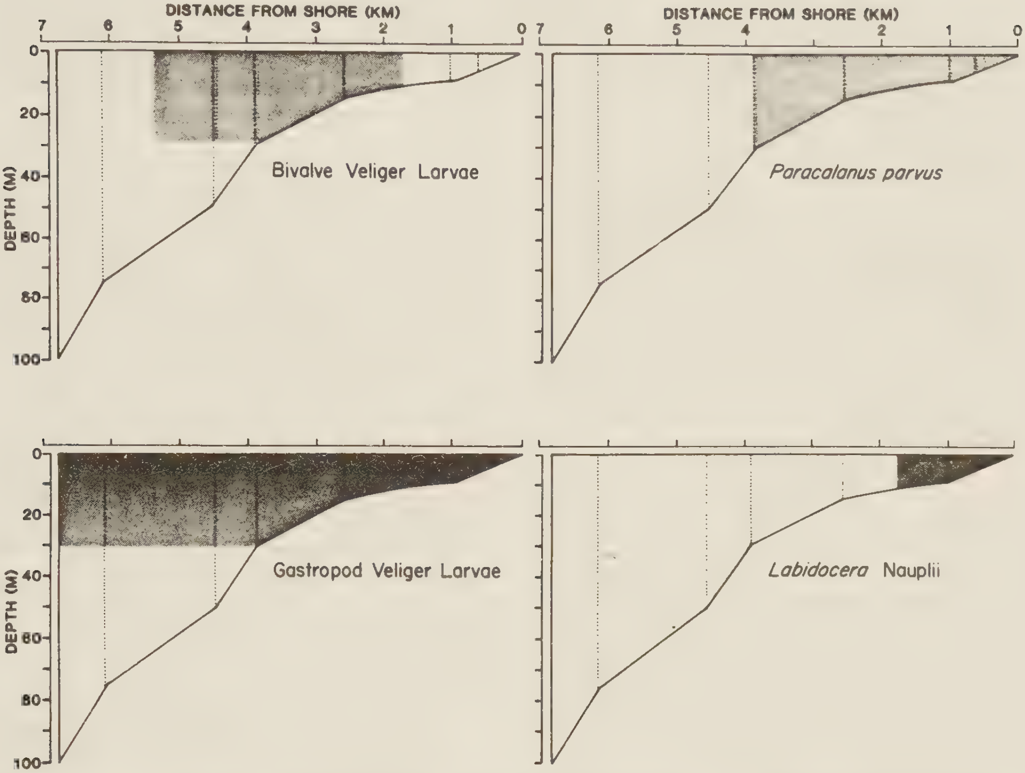

FIGURE 1.—Zones of significantly higher concentration of four zooplankton taxa near SONGS. Shaded areas represent higher concentration as determined by nonparametric one-way ANOVA ($P < 0.05$) on number per m^3 data. Redrawn from Marine Review Committee Document 78–01, Annual report to the California Coastal Commission, September 1977–August 1978: Updated estimated effects of SONGS Unit 1 on marine organisms. August 1978.

highest abundance in the neuston shoreward of the 9 m isobath.

Thus the distributions of the fish larvae and their prey are broadly similar. However, the sharp vertical gradients in abundance patterns for the atherinids and the older sciaenid larvae apparently do not closely match the vertical patterns of their prey. In discussing the results of their respective larval fish feeding studies, both of which utilized concurrent larval fish and zooplankton sampling during the day and night, Brewer and Kleppel (1986) and Jahn et al. (1988) remarked on this lack of a close match between the vertical distributions of fish larvae and their prey in the shallow nearshore zone. They suggested that factors other than, or in addition to, feeding must be important in determining larval distributions in the nearshore zone. Avoidance of dispersal seaward, away from the shallow coastal zone, is likely to be one of the most important factors (e.g., Brewer and Kleppel 1986).

Nearshore currents off southern California are mainly parallel to shore, tend to reverse at roughly tidal frequency, and have only a weak cross-shelf component (e.g., Winant and Bratkovich 1981; Jackson 1986). A comparison of the variances of the longshore and cross-shelf current speeds off San Onofre (the variance of the current speed is a good measure of the energy of the coastal current) indicates that the variance of the longshore current ($102\ cm^2/s^2$) is about four times that of the cross-shelf current ($25\ cm^2/s^2$) (Elwany et al. in press). This stronger longshore current has a net southerly motion, while the weak cross-shelf current has a net shoreward motion (Marine Review Committee 1977[5]). Thus plankters occupying the nearshore zone in the San Onofre vicinity will, on average, tend to be transported alongshore, but not out of the nearshore zone. Those plankters occupying the epibenthos, where currents are minimal, are especially likely to be retained in the nearshore zone (e.g., Barnett et al. 1984; Jahn and Lavenberg 1986; Barnett and Jahn 1987). At times, the nearshore plankton distributions at San Onofre are disrupted (Barnett and Jahn 1987), and during those times the neritic fish larvae may be transported seaward.

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[5] Marine Review Committee. 1977. Annual report to the California Coastal Commission, August 1976—August 1977, summary of the estimated effects on marine life of Unit 1,

Tidal mixing and nutrient recycling in the nearshore zone allows high rates of phytoplankton production near shore (Petersen et al. 1986; Barnett and Jahn 1987). This production can be utilized directly by fish larvae (e.g., Lasker 1975, 1981), or indirectly in the form of microzooplankton and small macrozooplankton, both of which occur in high concentrations near shore (e.g., Lasker 1978; Barnett and Jahn 1987). The nearshore zone appears to provide a good feeding environment for fish larvae, on average. However, it appears that this resource is largely utilized only by the nearshore species, since the larvae of more offshore species are relatively rare in the shallow coastal waters (e.g., Gruber et al. 1982; Barnett et al. 1984). Lasker (1975) demonstrated that the food resources of the nearshore zone may be critical to the first-feeding larvae of the broadly distributed species *Engraulis mordax*, and Theilacker (1986) showed that first-feeding larval *Trachurus symmetricus*, a more offshore species, were less vulnerable to starvation in nearshore habitats around the islands off the California coast than they were in offshore waters. However, larval *T. symmetricus* are uncommon in shallow coastal waters and in general there is little evidence that the shallow coastal zone provides an important feeding resource for the larvae of offshore fish species.

The observations that the larvae of the offshore fish species apparently make little use of the food resources of the nearshore zone, and that among the larvae of the neritic species the distributions of the larvae and their prey do not closely correspond, suggest that food is not the primary influence in determining nearshore larval fish distributions. What the primary influence (or influences) is remains to be determined. It does seem reasonable to conclude, at least, that larval fish distributions within the nearshore zone are a function of the advantages conferred by remaining in this environment.

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8880

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Seabird Relationships with Tropical Tunas and Dolphins

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Flocks of seabirds accompanying surface-schooling tunas are characteristic of tropical seas, but are especially notable in the eastern tropical Pacific (ETP) where the birds also associate with dolphins. We recently described these species interactions (Au and Pitman 1986) from extensive ship surveys that entailed the examination of cetacean schools, particularly those associated with birds and tuna. Our observations enabled us to form an ecological perspective of species behaviors and interrelationships. There have been few other studies on the oceanic ecology of ETP seabirds, although the birds are much watched by fishermen as indicators of fish and fishing conditions. King (1970, 1974a) and Gould (1971) presented the first comprehensive descriptions of tropical central and eastern Pacific birds at sea, but as their observations were primarily from ships conducting oceanographic surveys, they had limited opportunities for closeup observations of feeding flocks and were not able to study the relationships with cetaceans.

In this essay we review the relationships between seabirds, tuna, and cetaceans as observed in the ETP and describe the ecological role of tunas. We will explain how the organization of, and interactions within, the apex pelagic community might depend upon forage and foraging tactics, especially that of the tunas—perhaps the key top predators of tropical seas. Our inferences will be based largely upon the behavior of the birds and dolphins, as the tuna were seldom directly observable.

Data and Methods

Observations on birds, tuna, and cetaceans were obtained from both biological census and oceanographic ship surveys. Most important were the Southwest Fisheries Center (SWFC) dolphin surveys of 1976, 1977, 1979, and 1980, designed to assess the distributions and abundances of dolphins involved in the "porpoise-tuna" fishery of the eastern Pacific. These surveys provided information over a broad area overlapping the tuna fishing grounds. In addition to our participation on these biological surveys, Pitman studied birds, tuna, and cetaceans from ships conducting physical oceanographic studies in the central and eastern Pacific.

The search and much of the observations were conducted through twenty or twenty-five power binoculars, generally mounted both port and starboard on or above the flying bridge of each survey ship. We usually searched between 6 A.M. and 6 P.M., using two teams of observers. The high powered binoculars proved indispensable for closeup observations and for minimizing the overlooking of bird flocks and cetacean schools. On the dolphin surveys, most mammal schools were approached closely after initial detection for better observations (often within a hundred meters), as were bird flocks if they appeared to be associated with cetaceans. Flocks and schools were usually not approached on the oceanographic surveys. On all surveys, species were identified whenever possible, and numbers estimated for all flocks and mammal schools. We took notes on any tuna seen, but direct observations or measurements of these fish schools were not feasible.

Noon positions from the above cruises, shown in figure 5.1, illustrate survey coverage. The concentrations of survey days along certain lines is due to repeated hydrographic transects on the oceanographic cruises. Though there were surveys during every month, about 63 percent of the observations took place during January through March; there is thus a seasonal bias in our data. A monthly breakdown of observations is given by Pitman (1986), and a more detailed description of the dolphin surveys by Au and Perryman (1985).

Flock Characteristics

We defined a flock as an aggregate of ten or more birds. We did not include storm-petrels, phalaropes, tropic birds, or the occasional gulls, as they feed largely independently of fish schools in pelagic waters and rarely occur with either tuna or cetaceans. The 1977, 1979, and 1980 dolphin surveys provided the most representative and accurate subset of our observations; these data are summarized in table 5.1 (flock associations) and table 5.2 (flock composition) by 5° latitude intervals and according to eastern and western sectors. We sighted a total of 637 flocks in the eastern sector, and 125 flocks in the western sector (table 5.1). Overall, few (25 percent) of these flocks were with cetaceans, although the association rates were high in certain areas (see below). If we assume that flocks of ten or more birds are associated with tuna, most tuna schools, then, were not with cetaceans.

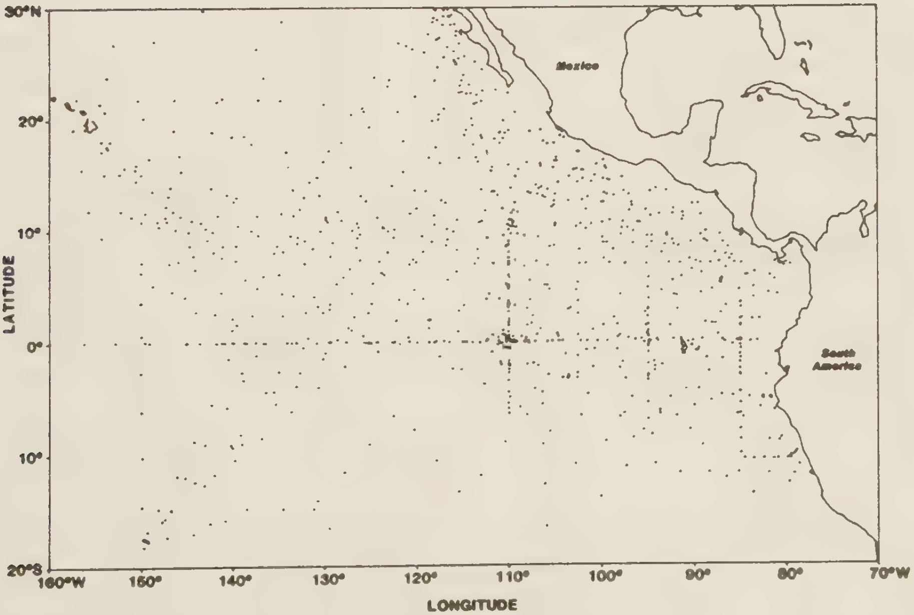

Figure 5.1. Noon positions of sea days during which a seabird watch was maintained.

Table 5.1. Percentage of seabird flocks associated with whale or delphinid cetaceans by area.

Center of 5° Latitude Intervals	EASTERN SECTOR (COAST-125°W)				WESTERN SECTOR (> 125°W–155°W)			
	Days observed	No. flocks	Pct. flocks with		Days observed	No. flocks	Pct. flocks with	
			whales	delphinids			whales	delphinids
25°N	16	6	0	0				
20°N	14	11	0	73	21	7	0	0
15°N	35	104	0	68	15	19	0	0
10°N	54	133	2	35	27	23	0	30
5°N	49	126	2	27	22	51	0	8
0°	38	108	2	4	11	13	0	0
5°S	14	80	0	5	7	6	0	0
10°S	11	69	1	7	8	5	0	0
15°S			0	0	5	1	0	0
Total	231	637	1	27	116	125	0	9

Notes: Flocks are defined as ≥ 10 birds; data from January–February cruises, 1977, 1979, 1980; percentages have been rounded; each latitude interval is defined by its center latitude ± 2.5°.

Table 5.2. Species composition and species diversity of flocks by area.

Sector	Center of 5° Latitude Intervals	Total Birds	PERCENT SPECIES COMPOSITION									SPECIES DIVERSITY	
			boobies	sooty tern	WTSW	jaeger	frigate birds	LPT	other terns	other shear-waters	other petrels	$\frac{1^{a}}{\Sigma Pi^{2}}$	Spp. per^{b} Flock
Eastern (From Coast to 125°W)	25°N	151				1	10			68	21	1.96	—
	20°N	1,279	15	3	8	1	+	2	22	46	3	3.46	4.4
	15°N	13,035	50	4	30	11	2	+	1	1	+	2.80	4.0
	10°N	6,852	14	28	32	13	8	1	1	2	+	4.40	4.2
	5°N	9,358	42	20	13	2	5	+	17	+	+	3.75	3.3
	0°	4,092	7	90	1	+	+	+	1	+		1.22	1.2
	5°S	3,696	+	94		+	2		4		+	1.12	1.3
	10°S	5,366	6	47		1	1	2	43		+	2.43	—
	15°S												

Western (From > 125°W to 155°W)	25°N												
	20°N	100	2	76			9	13				1.66	
	15°N	1,076	+	64	16	6		10	1	3	1	2.23	—
	10°N	3,355	+	69	8	2		19	+	1	+	1.92	3.0
	5°N	2,439	+	68	7	1		15	+	1	7	2.02	2.7
	0°	4,239		88	4	+		4	1	1	2	1.29	2.3
	5°S	6,983	1	97	1	+	1				1	1.07	2.2
	10°S	2,576	+	52	1		2	+	40	+	4	2.29	—
	15°S	1,538	+	40			1		57	+	2	2.07	—

NOTES: Flocks are defined as ≥ 10 birds; flocks were evaluated whether or not cetaceans were present; data from January–February cruises, 1977, 1979, 1980; percentages have been rounded: each latitude interval is defined by its center latitude ± 2.5°.

Abbreviations: WTSW = wedge-tailed shearwater; LPT = large pterodroma: Juan Fernandez/white-necked/dark-rumped petrels; + = small percent < 1.0.

[a] Simpson's Index.

[b] Mean spp. per flock weighted by flock size; dash indicates unreliable data; for dolphin-associated flocks, mean spp./flock was 4.4 (s = 2.0) in eastern sector and 1.9 (s = 1.2) in western sector (Au and Pitman 1986).

Dichotomy in the Pelagic Community

Two distinct faunal communities involving seabird flocks occur in the ETP, and suggest a strong, regional change either in prey or in the responses of predators to prey. The dichotomy separates multispecies flocks often associated with delphinid cetaceans from virtually single-species flocks seldom with delphinids (i.e., dolphins and other small, toothed "whales"). This separation occurs between latitudes 0° and 5°N and approximately corresponds with the oceanographic division between the permanently warm (> 25°C) and low salinity (< 34°/p.p.t.) Tropical (Surface) Water and the Equatorial (> 34°/p.p.t.) and Southern Subtropical (> 35°/p.p.t.) waters (see Wyrtki 1966; Ashmole 1971).

Northern (Tropical Water) Flocks

The Northern, or Tropical Water, flocks in the eastern sector were notable for frequently being with delphinid cetaceans: 68 percent and 73 percent of flocks from the 15°N and 20°N (± 2.5°) latitude intervals, respectively, were with delphinids (table 5.1). Associations with whales in these latitudes were infrequent (0–2 percent). These flocks (table 5.2) were typically multispecies aggregates of boobies—primarily red-footed *(Sula sula)*, masked *(S. dactylatra)*, and brown *(S. leucogaster)*—and wedge-tailed shearwaters *(Puffinus pacificus)*, sooty terns *(Sterna fuscata)*, and jaegers *(Stercorarius* spp.) (see appendix 5.1 for a list of species names). Boobies were most abundant, composing 42 percent and 50 percent of individuals in flocks in the latitude intervals centered at 5°N and 15°N. Their reduced importance about the 10°N interval was due in part to sampling near the Costa Rica Dome, a localized upwelling regime (Wyrtki 1964) that does not normally produce good catches of yellowfin tuna (the significance of which will be explained below).

In the western sector the northern flocks were associated with delphinids mainly within the 10°N interval (a much narrower zonation than seen to the east) where the association rate was 30 percent. As in the east, whales appeared unimportant to seabirds; none were seen with flocks. The species composition of these flocks was different from that of flocks farther to the east, and thus comprised a second type of multispecies community consisting mainly of sooty terns and Juan Fernandez/white-necked petrels (*Pterodroma externa externa/cervicalis*—subspecies that are difficult to separate in the field).

Southern (Equatorial and Southern Subtropical Water) Flocks

South of the 5°N latitude interval, in Equatorial and Southern Subtropical waters, but primarily the latter, flocks in the eastern sector occurred infrequently with delphinid cetaceans (table 5.1), in sharp contrast to the northern multispecies flocks. The southern flocks were clearly dominated by sooty terns (table 5.2) which composed 90 percent or more of birds in flocks in the 0° and 5°S latitude intervals, mainly in the areas away from islands.

In the west none of the southern flocks encountered were associated with either delphinids or whales. The sooty tern was still the most abundant species, up to 97 percent of the birds in all flocks. White terns *(Gygis alba)* and noddy terns (*Anous* spp.) were an increasing component of the flocks in the far southern latitudes; the latter terns were especially abundant near islands.

Species Diversity Differences

The transition and difference between the northern and southern seabird communities are reflected in latitudinal changes in species diversity. Values of Simpson's Dominance Index $\frac{1/\Sigma p_i^2}{p_i^2}$ where p_1 is the fraction of total birds that are species i) and of the average number of species per flock are given in the last two columns of table 5.2. Here the index could vary between 1.0 for flocks completely dominated by one species to 9.0 for flocks with individuals evenly divided among all nine categories of species. Simpson's Index is one of the more useful and easily understood measures for describing species in communities (Hill 1973) and shows that flocks in the northern latitude intervals, 20°N to 5°N, were on average 3.1 to 1.7 times more diverse than were flocks in the intervals 0° and 5°S, in the eastern and western sectors respectively. The southern flocks had index values close to 1.0 due to dominance by sooty terns. Data in the species per flock column suggest a decline in the average number of species from northern to southern latitudes (from ca. 4 to 1 spp./flock), at least in the eastern sector. Although there were difficulties in observing and identifying species from non-dolphin-associated flocks, this measure indicates areawide changes in diversity similar to those shown by Simpson's Index.

Seabirds and Cetaceans

As a group, seabirds associate only with specific cetaceans, a fact reflecting an underlying, probably feeding, relationship. This is shown in table 5.3, a summary of schooling and bird association characteristics of ETP whales and delphinids, again mainly from the more representative 1977, 1979, and 1980 dolphin surveys. Study of this table will give the reader an appreciation of the structure of the pelagic community under discussion, including the relative abundance of the different Cetacea and the likelihood (percent occurrence) of finding particular bird species in the associated flocks. In judging relative abundance, however, one should remember that different species vary in their detectability according to their size (school and individual) and behavior (including association with birds).

Associations with Dolphins

Of all Cetacea, spotted *(Stenella attenuata)* and spinner *(S. longirostris)* dolphins are associated most often with birds: 74 percent and 78 percent, respectively, of these species' schools were with flocks (table 5.3: first two species, col. 6). A high percentage of these schools included other cetaceans, 79 percent in the case of the spinner dolphin (col. 5). Most of this mixing involved these two species themselves: of the 113 spinner dolphin schools, 67 percent were mixed with spotted dolphins and of 206 spotted dolphin schools, 37 percent were mixed with spinner dolphins. Both of these dolphins occurred in large schools, averaging 150 and 133 individuals respectively (col. 3), and were associated with large flocks averaging 121 and 147 birds respectively (col. 7). The standard deviations (s) of these measures were large relative to the means, due to size distributions skewed toward the larger sizes. The bird species most likely present (high percent occurrence) in flocks with these dolphins were boobies (*Sula* spp.), frigate birds (*Fregata* spp.), wedge-tailed shearwaters, and jaegers, generally in that order. Spotted and spinner dolphins are diurnally active—i.e., fast swimming ("porpoising"), leaping often—and are frequently associated with yellowfin tuna. Both are pursued by purse seiners in "porpoise-tuna" fishing, a technique in which tuna are first caught with dolphins, then retained as the mammals are subsequently released.

Table 5.3. Summary of cetacean species encountered and their associations with seabirds: Characteristics of schools and flocks.

	SCHOOLS					ASSOCIATED FLOCKS			
SPECIES	*n*	$\bar{x}$	*s*	*Pct. mixed*[a]	*Pct. with flocks*	$\bar{x}$	*s*	*Spp. of > 50% occur*[b]	COMMENTS
Spotted dolphin *(Stenella attenuata)*	206	150	177	40	74	121	219	booby –82% frigate –70 WTSW–57 jaeger –53	Main target of "porpoise-tuna" fishing; diurnally active (leaping, fast swimming) sp.; mixed schools usually with spinner dolphin. Frequently with flocks; epipelagic prey (Perrin et al. 1973).
Spinner dolphin *(Stenella longirostris)*	113	133	207	79	78	147	258	booby –73% frigate –69 jaeger –62 WTSW–54	Second most important dolphin in "porpoise-tuna" fishing; diurnally active, usually mixed with spotted dolphins; frequently with flocks. Epi- and mesopelagic prey (Perrin et al. 1973).
Common dolphin *(Delphinus delphis)*	62	129	176	6	39	38	46	booby –70%	Less involvement in "porpoise-tuna" fishing; often escapes with tuna from nets; very active diurnally; third most frequent dolphin with flocks. May feed on deep prey (Fitch and Brownell 1968).

Table 5.3. (continued)

SPECIES	SCHOOLS					ASSOCIATED FLOCKS			COMMENTS
	n	$\bar{x}$	s	*Pct. mixed*[a]	*Pct. with flocks*	$\bar{x}$	s	*Spp. of > 50% occur*[b]	
Striped dolphin *(Stenella coeruleoalba)*	139	54	62	9	7	15	24		Common, diurnally very active species in relatively small schools; seldom with birds or tuna. May feed on mesopelagic prey (Miyazaki et al. 1973).
Bottlenose dolphin *(Tursiops truncatus)*	119	25	59	41	13	11	12		Often with *Globicephala, Grampus, Steno*; sometimes with *Stenella*; often approaches ships; not with large flocks.
Risso's dolphin *(Grampus griseus)*	106	11	18	20	3	16	17		Often with *Tursiops, Globicephala*, traveling slowly. Seldom with birds.
Pilot whale *(Globicephala macrorhynchus)*	98	14	12	37	4	11	11		Often with *Tursiops, Grampus*; appears to be resting much of the time. Seldom with birds.
Rough-toothed dolphin *(Steno bredanensis)*	54	12	10	15	35	12	15	booby –72% frigate –72	Sluggish behavior; often near flotsam; sometimes with *Tursiops, Globicephala, Grampus*; fourth most frequent dolphin with birds.

Melon-headed whale *(Peponocephala electra)*	4 [42	194	151	75 17	25 7]^c	1	—	Diurnally active; often in large, dense schools with *Lagenodelphis*. Seldom with birds.
Fraser's dolphin *(Lagenodelphis hosei)*	10 [23	391	576	40 44	20 13]^c	2	—	Often in large, densely packed, fast-moving schools with *Peponocephala*. Schools often execute coordinated turning and diving.
Pygmy killer whale *(Feresa attenuata)*	9	37	18	0	0	—	—	Appears to rest during the day; may approach ships. Seldom with birds.
False killer whale *(Pseudorca crassidens)*	19	13	13	26	10	12	5	Sometimes with *Tursiops*; will approach ships at high speeds; not with large flocks.
Killer whale *(Orcinus orca)*	8	7	4	12	12	20	—	Small schools, usually loosely aggregated; not with large flocks.
Rorquals (baleen whales)^d	94	2	1	3	3	43	27	Generally feed near surface on small fish and crustaceans; seldom with birds.
Ziphiids (beaked whales)	85	2	2	1	0	—	—	Deep feeder; shy and inconspicuous. Not with birds.
Sperm whale *(Physeter macrocephalus)*	63	8	7	8	2	2	—	Deep feeders; sometimes in large aggregations. Rarely with birds.
Dwarf/pygmy sperm whale *(Kogia spp.)*	30	2	1	0	0	—	—	Difficult to see except in calm seas. Not with birds.

NOTES: Numbers in table rounded for greater clarity; standard deviations not calculated for $n < 10$; birds counted regardless of flock size; n = number of schools, $\bar{x}$ and s refer to school or flock size.

Abbreviations, *see* table 5.2.

[a] i.e., school mixed with other cetacean sp.

[b] Listed here are bird spp. and their percentage occurrence in flocks associated with the given cetacean sp., provided the percentage was ≥ 50 and flocks ≥ 10 birds. WTSW = wedge-tailed shearwater.

[c] From larger sample from all research ship observations, and also including *Feresa* schools.

[d] Mostly Bryde's whale.

The common dolphin *(Delphinus delphis)* was the third most frequent species of dolphin found with bird flocks, although the percentage of its schools found with flocks was much lower (39 percent). This species also forms large ($\overline{x} = 129$), actively porpoising schools. Boobies, and also wedge-tailed shearwaters and frigate birds, often occurred in flocks associated with this dolphin. Fishermen do not regularly catch tuna with the common dolphin.

The last of the more frequently encountered, active delphinids, the striped dolphin *(Stenella coeruleoalba)*, is seldom found with birds. It usually occurred in fast-moving and often high-leaping, relatively small, unmixed schools ($\overline{x} = 54$) that were without indications of associated tuna. It is seldom deliberately fished on by purse seiners.

With two exceptions (see below) the remaining delphinids occur in small schools that are seldom with birds, and perhaps never with large flocks. Except for the false killer whale *(Pseudorca crassidens)*, all are relatively slow moving. And although the sluggish-behaving rough-toothed dolphin *(Steno bredanensis)* would seem to be an exception in that 35 percent of its schools were recorded with birds, we saw no evidence to indicate that this or any other other of these remaining dolphins occurred with tuna.

The melon-headed whale *(Peponocephala electra)*—sometimes called the electra dolphin—and Fraser's dolphin *(Lagenodelphis hosei)* are also seldom with birds, but yet they are like the bird-associated spotted and spinner dolphins in being diurnally active, fast moving, and in large schools ($\overline{x} = 194$ and 391, respectively), often mixed together. A sample from all research ship sightings between 1976 and 1981 that included all schools that were at least very likely either *Peponocephala* or *Feresa attenuata* (pygmy killer whale)—two species difficult to distinguish—gave twenty-three *Lagenodelphis* schools, of which only 13 percent were with bird flocks, and forty-two either *Peponocephala* or *Feresa* schools, of which only 7 percent were with birds (see bracketed results in table 5.3). It is clear, therefore, that birds are not strongly associated with any of these three dolphins.

Associations with Whales

We sighted many species of whales, and found they are generally not associated with birds (table 5.3). The rorquals we observed included blue *(Balaenoptera musculus)*, minke *(B. acutorostrata)*, sei *(B. borealis)*, and Bryde's *(B. edeni)* whales; these occurred singly or in small groups, all rarely with flocks. The ziphiid, or beaked whales, were also in small groups and were never seen with birds. Sperm whales *(Physeter macrocephalus)*, occasionally in large groups, were only rarely with birds. The related pygmy/dwarf sperm whales (*Kogia* spp.) were not seen with birds.

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Seabirds, Dolphins, and Yellowfin Tuna

The Predominance of Spotted/Spinner Dolphins with Seabirds

Clearly, only spotted and spinner dolphins in the ETP are commonly associated with seabirds, an indication of underlying behavioral interactions that are very species specific. This predominance is made clear in figure 5.2, which shows the percentage of schools of the different dolphins that were with flocks, as well as the percentage of all associated flocks occurring with each dolphin species. Separate histograms are given for latitudes 5°N to 30°N (Tropical Water) and < 5°N to 12°S (Equatorial and Southern Subtropical waters). Among the spotted and spinner dolphins, in mixed or in pure schools, schools with spotted dolphins were usually most often with birds, particularly in the 5°N to 30°N Tropical Water.

The relationship of birds to spotted dolphins appears to be stronger than that of birds to spinner dolphins. Of the 242 flocks in table 5.3, 63.2 percent were associated with at least some spotted dolphin as opposed to 43.0 percent with at least some spinner dolphin. Also, 34.7 percent of these flocks were with unmixed spotted dolphin but only 10.3 percent with unmixed spinner dolphin schools. Most spinner dolphin schools associated with birds (78 percent of 113 = 88 schools; table 5.3) were also with spotted dolphins (76.1 percent of 88). Flocks were less likely to be with unmixed spinner dolphin schools in northern tropical waters and more likely in waters to the south (figure 5.2). This was because most bird-associated spinner schools in the northern waters were also with the spotted dolphin.

While this strong relationship of seabird flocks to spotted and spinner dolphins is characteristic of the Tropical Water habitat north of the equator, and also of the area south of the Galapagos Islands during the southern summer (December to February), these dolphins are relatively infrequently with birds elsewhere (compare the two latitude intervals in figure 5.2). This is so particularly in areas southwest of the Galapagos Islands, in spite of the abundance of flocks there. Table 5.4 shows the reduction in equatorial and southern latitudes of both the schools of these two dolphins and the percent of these schools that were associated with flocks of more than ten birds.

The Yellowfin Tuna Link

Tuna Under Flocks

Seabirds in flocks appear to feed mainly on prey driven to the surface by tunas, which are the only sizable pelagic fishes known to form abundant and large surface schools in the tropical ocean. Not infrequently we have been able to identify the predatory fish under

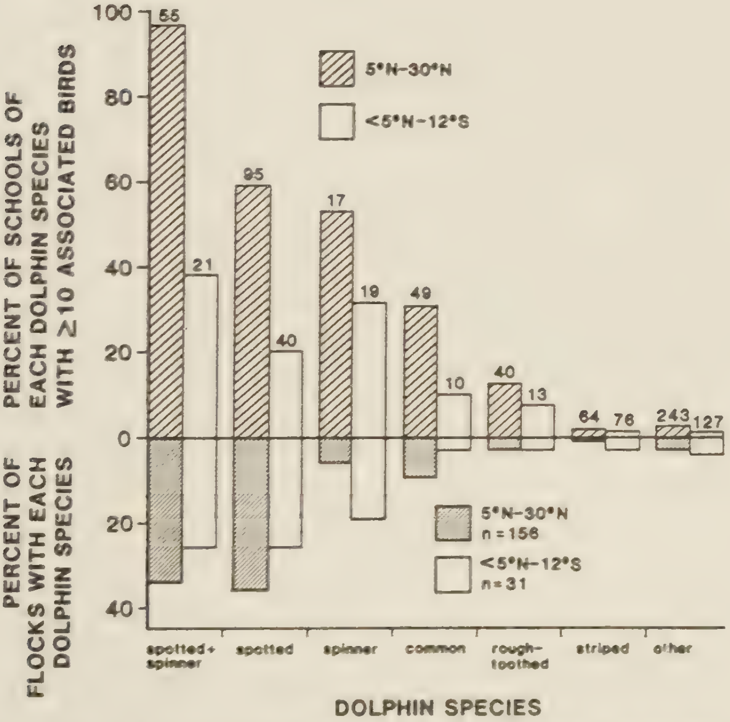

Figure 5.2. The rate of association of different dolphins with bird flocks (above) and the percent of these dolphin-associated flocks with each dolphin species (below) Numbers over the bars are the schools examined.

Table 5.4. Areawide differences in the percentage of spotted and spinner dolphin schools with bird flocks.

Center of Latitude	COAST TO 125°W			> 125°W TO 155°W			TOTALS		
		Schools with flocks			*Schools with flocks*			*Schools with flocks*	
Intervals	*Schools*	*n*	%	*Schools*	*n*	%	*Schools*	*n*	%
20°N	9	3	33				9	3	33
15°N	76	51	67				76	51	67
10°N	50	33	66	11	5	46	61	38	62
5°N	67	32	48	3	3	100	70	35	50
0°	28	3	11	3	1	33	31	4	13
5°S	15	3	20	1	0	0	16	3	19
10°S	6	5[a]	83	3	0	0	9	5	56
Total	251	130		21	9		272	139[b]	

NOTES: Data from research cruises in 1976, 1977, 1979, 1980; some schools near land are deleted; flocks are of size ≥ 10 birds. Each latitude interval is defined by its center latitude ± 2.5°.

[a] These associated flocks were encountered south of the Galapagos Islands and west of Peru, where the porpoise-tuna fishery extends during the southern summer.

[b] 58.8% of schools in latitude intervals ≥ 5°N (± 2.5°) were with flocks of size ≥ 10; only 21.4% of schools in latitude intervals < 5°N (± 2.5°) were with such flocks. This differential is significant (X^2, $P < 0.005$).

a feeding flock as tuna (see also Murphy and Ikehara 1955; Ashmole and Ashmole 1967). The strongest evidence linking birds and dolphins to tuna is the existence of the "porpoise-tuna" fishery of the eastern Pacific, in which purse seiners catch yellowfin and to a lesser extent skipjack *(Katsuwonus pelamis)* tuna that swim with dolphins. These tuna, and the associated dolphins, are found mainly by searching the horizon for birds. Spotted, spinner, and common dolphins (ranked by importance) are the primary cetaceans involved in that fishery (Hammond 1981; Smith 1979). These are the same species, and order of importance, of dolphins that are associated with bird flocks, indicating that birds and dolphins are associated because of a tuna relationship.

The "Porpoise-Tuna" Fishery

The extent of the fishing grounds for surface-caught yellowfin is shown in figure 5.3 with the distribution of sightings of spotted dolphin superimposed (the distribution of spinner dolphin is nearly the same). The similarity of these distributions indicates an intimate species interaction, although such a result could be an artifact of joint fishing on both species by the purse seiners that supplied the data to the SWFC. However, the general pattern of the dolphin distribution has been confirmed by fishery-independent surveys (Au and Perryman 1985). Dolphin-associated yellowfin tend to be large ($\bar{x} = 120$ cm, s = 22 cm, years 1981–85) (see also Allen 1985) with sizes overlapping into the range of smaller yellowfin not caught with dolphins and of larger, deep-dwelling yellowfin that are caught by longline gear. Appendix 5.2 shows the relationship between tons of yellowfin caught and sizes of the associated dolphin schools on the purse seine grounds. The porpoise-tuna fishery indicates that seabirds and dolphins are linked via a relationship (probably feeding) with large yellowfin tuna.

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The Ecology of Flocks

Species in Dolphin-Associated Flocks

Composition

The species composition of dolphin-associated flocks shows the same regionwide differences among flocks in general. The important bird species that make up flocks associated with spotted and spinner dolphins are shown in figure 5.4, where again the histogram is separated for latitudes 5°N to 30°N and 5°N to 12°S. As in table 5.2, boobies, wedge-tailed shearwaters, jaegers, sooty terns, and frigate birds were numerically most important, in that order, in the dolphin-associated flocks from the northern Tropical Water habitat (5°N–30°N).

In the southern waters (< 5°N–12°S) boobies and sooty terns predominated; however, they were not usually in the same flocks. Boobies occurred mainly in flocks not too distant from coasts, while the sooty tern—more usually in virtually single-species flocks not with dolphins—was characteristic of the far offshore flocks (tables 5.1, 5.2).

Species Associations

Boobies, wedge-tailed shearwaters, jaegers, and frigate birds were found to be positively associated in dolphin-associated flocks from the Tropical Water purse seine fishing grounds, while frigate birds and sooty terns were positively associated in mainly the outer areas

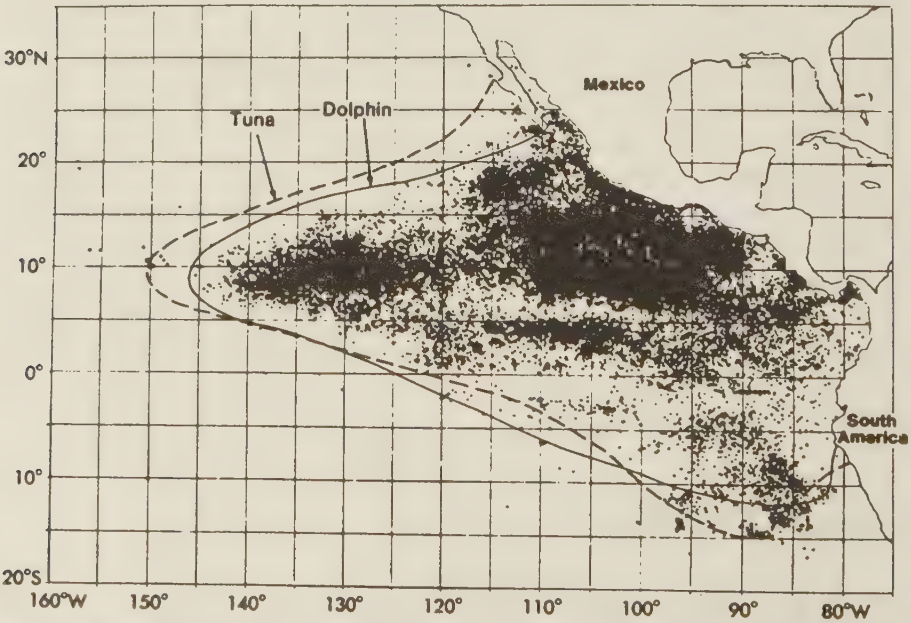

Figure 5.3. The distribution of records of spotted dolphins (dots and solid boundary, after Perrin et al. 1983) in relationship to the yellowfin tuna purse seiner grounds (dashed boundary, after Calkin's [1975] map of areas that produced 25+ tons of yellowfin catch).

of that habitat (Au and Pitman 1986). Table 5.5 is an extract of that analysis, showing percent co-occurrence of different bird species both in those flocks in which the species occurred, and in all flocks. The significant positive associations are also indicated. A schematic interpretation of this association complex is given in figure 5.5, where two measures of strength of association between species pairs are presented: Cole's (1949) coefficient and Yule's contingency index (see Pielou 1969:164). Our data indicate that none of the associations are very strong. The figure suggests that frigate birds are positively associated with other species in all habitats. The simplest explanation of these positive associations is attraction to common feeding opportunities.

Feeding Tactics/Strategies

Multispecies Flocks and Facultative Commensals

Within multispecies flocks, simultaneously different, species-specific feeding behaviors suggest prey aggregations that are diverse

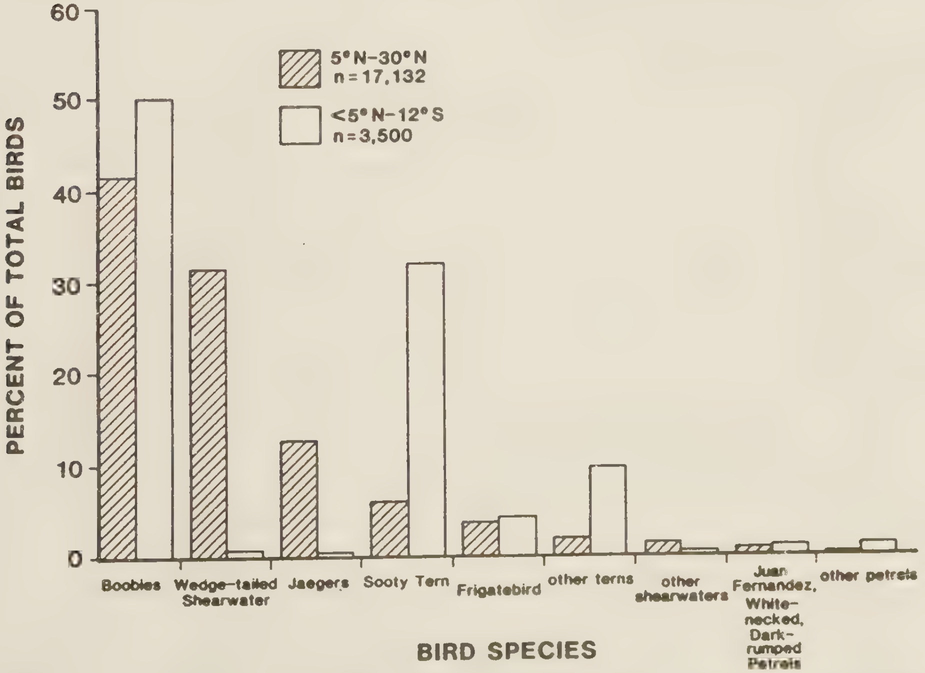

Figure 5.4. Likelihood (percentage frequency) of finding bird species in flocks associated with spotted and spinner dolphins.

Table 5.5. Percentage of co-occurrence of species pairs in flocks.

		Boobies *n = 111*	*Frigate Birds* *n = 90*	*WTSW* *n = 82*	*Large Pterodromas* *n = 18*	*Jaegers* *n = 80*
Sooty tern	% n	45	53*	49	56	46
	(% total)	(38)	(37)*	(31)	(8)	(28)
Boobies	% n		90*	90*	44	92*
	(% total)		(62)*	(56)*	(6)	(56)*
Frigate birds	% n			72	50	75
	(% total)			(45)	(7)	(46)
WTSW	% n				50	74*
	(% total)				(7)	(45)*
Large Pterodromas	% n					11
	(% total)					(7)

NOTES: From $n = 131$ flocks associated with spotted or mixed spotted and spinner dolphin schools in latitudes 5°N–30°N in the eastern Pacific; example: sooty terns co-occurred with boobies in 45 percent of the 111 flocks containing boobies, and in 38 percent of all 131 flocks; * indicates a significant positive association between the species pair (by X^2, $P < 0.05$); there were no significant associations detectable among the thirty-three spotted/spinner dolphin–associated flocks from latitude < 5°N.

WTSW = wedge-tailed shearwater.

with respect to behavior, distribution in the water column, size, or species composition (we will refer to this diversity as prey "configuration"). Boobies, flying rapidly back and forth, especially over the advancing front of a tuna school, wheel and plunge after their prey or make midair captures. Wedge-tailed shearwaters seemingly race with the boobies, but at lesser heights, and then drop to the water in surface plunges or for contact dipping or surface seizing of prey that appear available for at least several seconds. Jaegers, taking prey by aerial pursuit and dipping, and occasionally by piracy, add to the scene of frantic activity (feeding methods are defined by Ashmole [1971]). By rapidly covering the school, birds of each species increase their encounter rate with unpredictably available and fleeting prey. Sooty terns employ another tactic—they watch widely and deep into the water for developing feeding opportunities from positions high above. Their prey appear to be grouped, for the entire

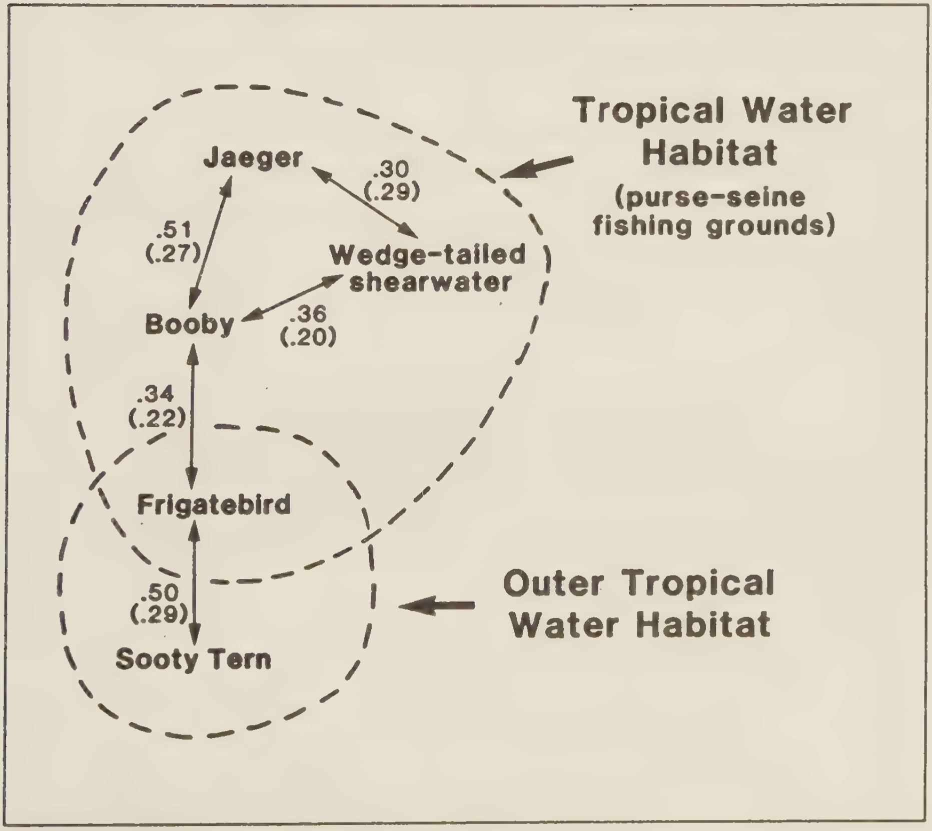

Figure 5.5. Positive species-association links within flocks, with strength-of-association coefficients (Cole's and Yule's [in parentheses] coefficients) shown.

flock will swoop down synchronously. Frigate birds soar high above the feeding melee and swoop down at opportune moments after individual prey that are likely larger than that of the terns.

Except for sooty terns and frigate birds, most birds that occur in these multispecies flocks are facultative commensals with tuna. When feeding independently, these birds occur singly or in small groups, and aerial feeding is rarely seen. Petrels and shearwaters, for example, then rely more on scavenging or preying upon free-floating organisms such as *Velella* (Pitman personal observations). Boobies, however, appear to feed independently of tuna the least, and their distribution most closely coincides with that of the yellowfin tuna fishery (cf. figures 5.3 and 5.6, considering also the low-density, westward extension of booby habitat [below]). Boobies are both the most abundant of birds in flocks over tuna and dolphins (figure 5.4) and the most abundant of seabirds in the northern Tropical Water (Pitman 1986), with colonies in the eastern Pacific that are probably the world's largest (Nelson 1978). The abundance of boobies is likely a direct consquence of their strong association with yellowfin.

"Obligate" Commensals

In contrast to the facultative commensals, sooty terns and frigate birds are almost never seen feeding independently of tuna in oceanic

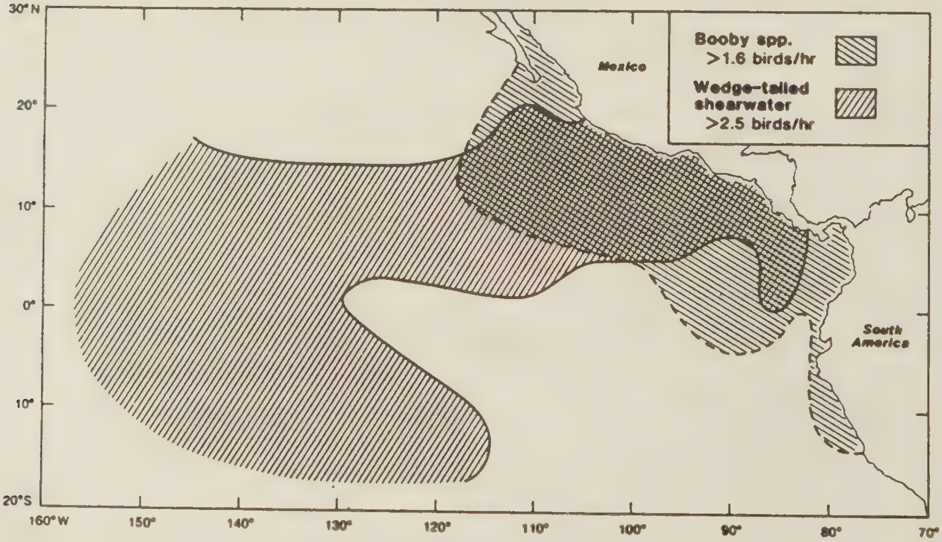

Figure 5.6. Booby and wedge-tailed shearwater habitats. Each shaded area delimits regions of greater than median sighting rate of the species (birds/hour). After Pitman 1986.

areas; they appear to be near-obligate commensals with these fish. The sooty tern, in particular, is most abundant beyond the yellowfin fishing grounds, where the tuna it feeds with are generally small, probably skipjack (Hida 1970), but possibly also frigate mackerel (*Auxis* spp.; see Olson and Boggs 1986) or small yellowfin and bigeye tuna *(Thunnus obesus)*. It is the most abundant seabird of the southeastern and central Pacific (Pitman 1986; Gould 1974). In the former area, there is apparently little opportunity for feeding independently of tunas; facultative commensals (i.e., most other birds) are virtually excluded from those waters, apparently being unable to feed either with sooty terns or independently (table 5.2 and below). The obvious ecological success of the sooty tern probably stems from its ability to follow and feed with the small tuna.

Feeding Regimes

Species Distribution

Distinctly different distributions of four birds that occur in flocks illustrate how the community dichotomy is formed from seabirds that seem to feed differently. The distributions are depicted in figures 5.6 and 5.7, where a single contour is used to enclose areas of higher population density of each species. These were derived from distribution and relative abundance studies by Pitman (1986). Each species' contour approximately delimits areas where densities were greater than that species' median sighting rate (birds per hour). Figure 5.6 shows boobies and wedge-tailed shearwaters inhabiting the Tropical Water north of the equator, but seldom occurring in a large area of the southeastern tropical Pacific west of the Peru Current. The habitat of the wedge-tailed shearwater extends into the eastern Pacific from broad areas to the west, while that of boobies extends from the east, westward with the yellowfin tuna fishing grounds. The lower-density (less than median sighting rate) habitat of boobies (primarily the masked booby) extends far west of Clipperton Island—at 10°N, 109°W (Pitman 1986) (this is not shown clearly in figure 5.6 because areas of greater than median sighting rate of boobies, especially the red-footed booby, are compressed toward the American coasts). Figure 5.7 shows an extensive high-density area of the sooty tern habitat in the central Pacific, extending into the Subtropical Water of the southeastern Pacific, the area with a dearth of boobies and wedge-tailed shearwaters. The high-density areas of this tern are sparse in the Tropical Water north of the equator. Finally, Juan Fernandez/white-necked petrels occur in a band about latitude 10°N, especially to the west of longitude 110°W.

Not shown is the jaeger habitat, mainly within a thousand-kilometer-wide band along the coast of Middle America, and the fact that the larger seabirds are relatively uncommon along the equator, being replaced there by plankton-feeding storm petrels. The distributions of the seabirds also vary seasonally; in particular, sooty terns probably extend farthest into the southeastern Pacific during the southern summer.

Regional Prey Differences

The northern (Tropical Water) and the southern (Equatorial and Southern Subtropical waters) habitats of the ETP thus appear to have different prey characteristics or configurations that require different foraging tactics, as indicated by community differences in seabird species and their interactions. In the northern Tropical Water, prey patches appear to be relatively large and to have diverse kinds of prey. Once found, hundreds of birds and dolphins (see table 5.3) and yellowfin (e.g., 10 tons of fish 60 lbs or greater; see IATTC 1984 and appendix 5.2) may feed upon the patch. Feeding many continue for some time (we have watched this activity for nearly an hour before continuing on). Under such conditions, satiated birds, e.g.,

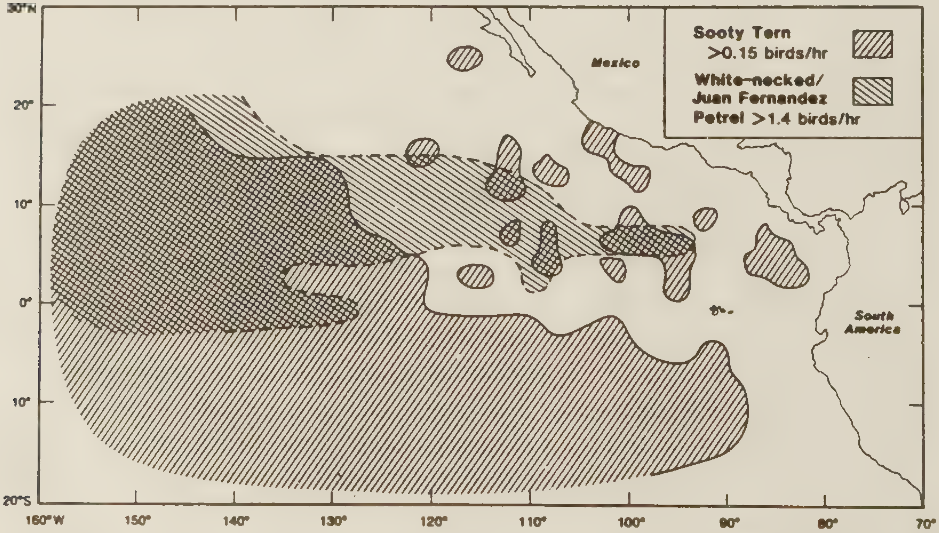

Figure 5.7. Sooty tern and white-necked/Juan Fernandez petrel habitats. Each shaded area delimits regions of greater than median sighting rate of the species (birds/hour). After Pitman 1986.

boobies, petrels, and especially shearwaters, may rest upon the water while others continue to feed (personal observation). In contrast, prey in the less productive southeastern and central Pacific appear to be in small, ephemeral, and thinly scattered patches of simple configuration, judging by the behavior and composition of feeding flocks. The buoyantly flying sooty tern especially, which is unable to rest long, or at all, upon the water, is evidently adapted for exploiting such prey, whose availability appears to change quickly, lending few opportunities for heavy feeding. These habitat differences probably reflect dissimilarities in biological productivity. The northern Tropical Water is richest because of its proximity to land and mechanisms that carry nutrients across its strong, shallow thermocline (Brandhorst 1958; Wyrtki 1966).

Pertubations

If prey characteristics select for particular bird-tuna-dolphin interactions, environmental perturbations could alter these behaviors through effects on forage. During the 1982–83 El Niño warming event in the Pacific (Philander 1983), fishermen experienced a 25 percent reduction in the yellowfin tuna catch (IATTC 1984) and reported fewer porpoise-tuna schools. Because El Niño episodes usually result in reduced biological production and a deepened thermocline (see Barber and Chavez 1983), a weakened tuna-dolphin association might be expected, as is characteristic of the deep-thermocline and less productive southeastern and central Pacific. We looked for such effects in the characteristics of flocks recorded off Middle America (from Baja California to the equator) in 1979, 1980, and 1983. Records of all flocks and of flocks associated with spotted, spinner, and common dolphins were examined. These data, summarized in table 5.6, suggest that flock density was similar over the years, as was species composition: boobies and wedge-tailed shearwaters were always most abundant. However, flock size, dolphin school size, the percent of dolphin schools with birds, and the ratio of size of dolphin-associated flocks to that of all flocks were all much reduced in 1983. Although the 1983 sample was probably too small to be representative, these reduced percentages in 1983 are consistent with the idea that decreased food production or availability near the surface results in tuna feeding more independently of dolphins and in ways that are less useful to birds.

General Discussion

It is curious that the association of seabirds, yellowfin tuna, and dolphins is so specific to spotted and spinner dolphins; the birds essentially ignore the twenty or so other species of Cetacea in the eastern Pacific. This is somehow related to the conspicuous partitioning of the eastern tropical Pacific (ETP) into distinct epipelagic communities of differently interacting predators.

Foraging Tactics and Species Interactions

Tuna Strategy and Consequences

To begin understanding oceanic species interactions, it is useful to consider the behavior of the surface-schooling tunas. Tuna behavior exemplifies a strategy for exploiting the relatively sparse prey of tropical seas. Tropical tunas feed on epipelagic fish, squids, and crustaceans, whose distributions are undoubtedly very patchy with low overall densities (Blackburn 1968). To ensure a sufficient capture rate of such prey, tunas search by extensive ranging in the horizontal dimension, an energetically demanding tactic. Norberg (1977) postulated that as prey density decreases, the search method required of a predator increasingly becomes both more energy consuming and more efficient. Thus tunas have evolved into perhaps the most streamlined of fishes; their whole morphology and physiology appear designed for fast, sustained swimming with metabolic rates probably higher than those of all other fishes (see Sharp and Dizon 1978 for descriptions of energetics and hydrodynamics). High energy expenditure to obtain moderate energy returns from low-density prey must constrict the tunas' positive energy balance, narrowing the scope, or margin, between energy gained from food and energy consumed (see Warren and Davis 1966). Constriction of this energy margin increases vulnerability to natural mortality; for their size and speed, tropical tunas are remarkably short-lived, living probably less then ten years on the average (Beverton and Holt 1959).

These costs notwithstanding, the efficacy of the tunas' feeding strategy is evident; they are the dominant pelagic fishes of the tropical ocean, supporting extensive bird populations and productive fisheries. During the period 1974 to 1981 (between major El Niño events) an average of 196,000 metric tons of yellowfin tuna was harvested annually from the ETP, virtually all from surface or near-surface schools (IATTC 1984), approximately half of which were dolphin-associated (Allen 1985). In the same period, skipjack tuna produced an average annual catch of 122,000 metric tons, mainly from "schoolfish," i.e., surface schools without dolphins.

Feeding with Tuna

Seabirds that feed with surface tunas exploit the tunas' tactic for finding prey and their habit of driving it to the surface. This role was recognized by Ashmole and Ashmole (1967) and is the basis for fishermen's reliance on birds to locate these fish. The degree to which tuna schools are accompanied by flocks, however, is difficult to estimate, as most schools are detected only if associated with birds. Appendix 5.3 shows that whereas most schools fished ~~by~~ seiners were with birds (as expected), schoolfish tuna were both less often and more variably with birds (29 percent to 77 percent overall depending upon area).

Dolphins that associate with yellowfin tuna also may have a feeding relationship with these fish. The prey of the spotted dolphin is similar to that of yellowfin, both feeding diurnally upon epipelagic fishes and squids (Perrin et al. 1973; Reintjes and King 1953). Seabirds feed on much the same kinds of prey (Harrison, Hida, and Seki 1983; Diamond 1983). Spinner dolphins feed more on mesopelagic animals and may be less directly linked to tuna (Perrin et al. 1973). The ecological success of spinner and especially spotted dolphins in the eastern Pacific, which may be appreciated by comparing the numbers and average sizes of their schools with that of the

Table 5.6. Comparison of flock characteristics and interactions off middle America during three years.

	TOTAL				
Year	*Flocks*	*Birds*	*Hours observed*	*Flocks per hour*	*% Flocks with dolphins*
1979	136	10,366	270.0	0.5	27
1980	73	3,721	191.6	0.4	45
1983	25	800	49.0	0.5	28

Note: Dolphins referred to are spotted, spinner, and common dolphins.
WTSW = wedge-tailed shearwater.

other cetaceans (table 5.3), is likely due to a considerable advantage gained from feeding with yellowfin tuna.

Seabirds' Relationship to Cetaceans

In spite of the strong association of spotted and spinner dolphins with birds, our observations indicate that cetaceans themselves have little role in making prey available to seabirds. It is the tuna, primarily, that appear to drive prey to the surface, whether or not dolphins are present; foraging birds are almost always most active where the tuna are feeding, which often is at the leading edge of the school. This has been seen from ships (personal observation) and from helicopters (Au and Perryman 1982; Hewitt and Friedrichsen ms.). Thus spotted and spinner dolphins are commonly with birds because they swim with tuna with which the birds feed. And the common dolphin is relatively infrequently found with flocks because its association with tuna is similarly infrequent. Though the rough-toothed dolphin is not uncommonly associated with small flocks, it was probably the flotsam (and associated fish) near which this species was often encountered, rather than tuna or the mammals, that attracted the birds. Tropical seabirds thus appear to strongly associate only with those dolphins that swim and feed with tuna, dolphins that, like the tuna, are fast traveling and in large, diurnally active schools. Even so, these tuna and birds appear to feed independently of dolphins much of the time, as indicated by the delphinid association rate of flocks: between latitudes 2.5°N and 22.5°N, 58 percent of flocks (presumably with tuna) were not with dolphins (data for table 5.1, Eastern Sector). The tuna-dolphin association is

PERCENT SPP. COMPOSITION OF FLOCKS								FLOCK SIZE		DOLPHIN SCHOOLS	
Boobies	*Sooty tern*	*Other tern*	*WTSW*	*Other shear-waters*	*Jaegers*	*Frigate birds*	*Other birds*	*All*	*With dolphins*	*Size*	*Pct. With birds*
38	13	3	34	1	8	2	1	76.2	159.8	297.9	75
23	17	12	15	1	11	7	3	51.0	88.4	149.2	76
16	1	10	66	2	4	2	0	32.0	21.7	115.2	29

clearly not obligatory; it seems rather to indicate an intersection or overlap of certain foraging tactics adopted by these species to exploit local prey configurations.

Communities and Foraging Requirements

The foraging tactics required in a particular environment seem to shape communities by placing stringent demands upon the behavioral or energetic capabilities of predators, especially in biologically sparse waters. Thus while spotted and spinner dolphins regularly associate with large yellowfin tuna on the purse seine fishing grounds of the Tropical Water habitat, these tuna are largely unable to forage in the surface layer beyond those grounds, perhaps in part due to physiological needs (see Sharp 1978 for a detailed discussion), and the dolphins there seem unable to feed with the skipjack or other small tuna that replace the yellowfin. The multispecies flocks of both facultative and obligatory commensals that feed with yellowfin on the purse seine grounds are reduced to mainly sooty terns and wedge-tailed shearwaters in the biologically sparse waters of the central Pacific and to virtually sooty tern–only flocks, obigatorily commensal on small tuna, in the Southern Subtropical Water. Like other facultative commensals, wedge-tailed shearwaters, so widespread in the central Pacific (Pitman 1986; King 1974b), are apparently unable to assume the required feeding tactics and to penetrate the Southern Subtropical Water of the eastern Pacific (figure 5.6).

Who Follows Whom?

It is clear that seabirds follow and benefit from feeding with tuna, but where these tuna are also associated with certain dolphins, does either the tuna or dolphin provide benefit to the other? This question is pertinent to understanding the role of dolphins in bird-tuna-dolphin associations. A widely held view is that tuna follow dolphins in foraging. Tuna evidently do follow dolphins that are chased by purse seiners and are eventually captured with these schools. Mullen (1984) showed how two potentially competing predators could theoretically and stably coexist in a commensal relationship and suggested that the tuna were commensals on the dolphins. But perhaps tuna, and pelagic schooling fishes in general, obtain protection from pursuing predators by crowding under objects they normally encounter, both animate and inanimate—as when a predacious marlin approaches, skipjack will hide under the boat fishing them (D. Correa, personal communication). We suggested (Au and Pitman 1986) that spotted and spinner dolphins follow yellowfin in jointly foraging schools, inferring this mainly because seabirds are often seen feeding at the front of such schools in immediate association with the tuna rather than the dolphins. We note that the tuna-dolphin association breaks down outside the ETP purse seine grounds, where large yellowfin no longer commonly school at the surface (the dolphins must continue to do so, though they are no longer often with birds), and that a large tuna school, searching in three-dimensional space and perhaps using olfactory cues, could be more efficient than dolphins in locating prey.

In retrospect, it seems unlikely that a simple answer, either the dolphins or the tuna following the other to food, could be satisfactory. Neither is it likely that the tuna-dolphin-bird association merely results from the convergence of predator species upon the same food patches, for the association is too species specific, and tunas and dolphins appear to travel together, even while not actively feeding. Finally, no explanation can be satisfactory unless it also explains why the dolphin-tuna association is not characteristic of the eastern tropical Atlantic (Levenetz, Fonteneau, and Regalado 1980; Stretta and Slepoukha 1986), where a large purse seine fishery for surface yellowfin and skipjack tuna also exists, and dolphins similar to that of the ETP occur (Leatherwood, Caldwell, and Winn 1976).

A Feeding Tactics Hypothesis

Hypothesis

We propose a hypothesis that particular prey configurations or arrangements that are a function of productivity shape species interactions through the foraging tactics required to exploit that prey. The resulting explanation of species interactions is as follows: In low productivity waters, low-density prey are exploited by skipjack or similar small-sized tuna that are specialists at surviving on small prey from highly dispersed, relatively small patches. These patches are sufficiently encountered only through the most rapid and energetically expensive, wide-ranging search. Under such conditions smaller, rather than larger, predators are at an advantage (Norberg 1977). In accordance with foraging theory (Charnov 1976), these tuna employ, in effect, hit-and-run tactics on patches not much more profitable than from average searching between patches. Ecologically successful seabirds in such areas would be those capable of keeping up with these fast tuna, there being little food available independent of the fish.

In areas of intermediate food productivity, such as along oceanic boundary zones, food patches and prey are larger, though still best discovered by extensive horizontal ranging. Once found, these patches often provide for relatively long feeding bouts. Large yellowfin tuna and similarly foraging spotted and spinner dolphins find and exploit this prey, often jointly. When doing so, the tuna may be the primary predator, and they may drive some prey to the surface. Many birds take advantage of these enhanced feeding opportunities, forming multispecies flocks; however, most species in these flocks can also supplement their food by also feeding independently of tuna.

In still higher-productivity waters, such as coastal areas, prey is more diverse, the food encounter rate is high, prey patches are large and more predictable, and the advantage of the wide-ranging foraging tactic of tunas is lessened. It may sometimes be advantageous for tunas to forage passively—for example by waiting for prey under objects. The richer and less clumped food resources would enable the different predators to specialize and to feed more independently.

Extensions

The hypothesis would predict that reductions in food productivity would reduce the participation of all species involved in joint feeding, as suggested for 1983 in table 5.6 (this would not be expected if there were an obligate commensal relationship between tuna and dolphins). Moreover, the switching of feeding tactics and hence changes in community interactions might be the mode of response to such changes. Such a mechanism may have been involved in the massive population failure of seabirds from Christmas Island during the last El Niño (see Schreiber and Schreiber 1984).

The hypothesis suggests that intermediate productivity would be most conducive to the formation of multispecies interactions involving birds, tuna, and dolphins. In fact, the most extensive porpoise-tuna fishing areas in the eastern Pacific are not the rich coastal and upwelling-influenced waters off Central America, but the warm, stable waters off southern Mexico and the waters west of Clipperton Island. Areas where two-thirds or more of purse seine operations are on dolphin-associated yellowfin begin about 600 kilometers offshore (see Allen 1985), except off southern Mexico, where the fishing comes close to shore. Could it be that yellowfin tuna in the eastern tropical Atlantic are seldom associated with dolphins because waters there are not sufficiently intermediate in productivity to develop the right prey configuration? That fishery is located mainly in the Equatorial Counter and Guinea currents within 500 kilometers of the southern West African coast, an environment more similar to Pacific waters west of Panama and Colombia than to the ridged thermocline (Cromwell 1958), offshore porpoise-tuna grounds west and southwest of southern Mexico (see Merle 1978).

Background

This idea, that the resource base in different environments controls species interactions through the tactics required for its exploitation, is patterned after the concepts developed by Crook (1965) in a study on birds and as applied in comparative behavior studies of primates (Crook 1970; Clutton-Brock and Harvey 1977). These authors explained how the social organization and behavior of species are shaped by the availability of food and sites for reproduction. Smith et al. (1986), noting that common dolphins tended to occur in large, mobile schools in oceanic waters off California, while Dall's porpoise *(Phocoenoides dalli)* occurred in small, relatively sedentary schools in chlorophyll-rich, coastal waters, suggested that the behavioral and population differences were due to feeding strategies required of each species in the different environments. Differences in feeding behaviors of seabirds from Antarctic to tropical seas were explained by Ainley and Boekelheide (1983) as adaptations to regional differences in prey density and patchiness, as well as to the presence of subsurface competitors and predators. Wiens (1984) reviewed the importance of resources in the organization of avian populations and communities, noting how little direct evidence there was of resource limitation. He cautioned against imposing possibly preconceived processes, such as competition, on the analysis of relationships. However, Safina and Burger (1985) thought that terns in coastal waters could compete with bluefish by pursuing the same individual prey. We have not directly considered competition as a mechanism in our hypothesis. Until demonstrated, Schoener's hypothesis (1982) of predator convergence onto locally abundant prey patches, with little interspecies competition, seems more likely. Ours is an attempt to explain the existence in the eastern tropical Pacific of distinct pelagic communities, not separated by physical barriers, and composed of specific assemblages of highly mobile species with specific behavioral interactions.

Summary

Two distinct faunal communities involving seabirds may be recognized in the eastern tropical Pacific. One, characteristic of the Tropical Water habitat mainly north of latitude 5°N, consists of multispecies flocks of primarily boobies, wedge-tailed shearwaters, jaegers, and sooty terns. These flocks are frequently associated with large yellowfin tuna and dolphins. Of the dolphins, the spotted and spinner species predominate (ca. 75 percent of dolphin-associated flocks involve these two species). These dolphins appeared to be linked to birds because both feed with large yellowfin tuna wherever the latter forage close to the surface. The other community occurs primarily in Subtropical Water to the south and consists of virtually single-species flocks of sooty terns. These flocks are associated with small tuna but seldom with dolphins. We propose that the different kinds of species associations seen in the eastern Pacific are manifestations of different foraging tactics required of pelagic predators in the different areas, and that the intersection of such tactics could explain the bird-tuna-dolphin association.

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Appendix 5.1. Common and scientific names of species mentioned in text.

TUNAS	
Yellowfin	*Thunnus albacares*
Bigeye	*T. obesus*
Skipjack	*Katsuwonus pelamis*
Frigate mackerel	*Auxis* spp.
BIRDS	
Boobies	
Red-footed	*Sula sula*
Masked	*S. dactylatra*
Brown	*S. leucogaster*
Wedge-tailed shearwater	*Puffinus pacificus*
Sooty tern	*Sterna fuscata*
Jaegers	*Stercorarius* spp.
Juan Fernandez petrel	*Pterodroma externa externa*
White-necked petrel	*Pterodroma externa cervicalis*
Dark-rumped petrel	*Pterodroma phaeopygia*
White tern	*Gygis alba*
Noddy terns	*Anous* spp.
Frigatebirds	*Fregata* spp.
Phalaropes	(Phalaropodidae)
Storm-petrels	(Hydrobatidae)
Gulls	*Larus* spp.
Tropic birds	*Phaethon* spp.
CETACEANS	
Delphinids	
Spotted dolphin	*Stenella attenuata*
Spinner dolphin	*S. longirostris*
Striped dolphin	*S. coeruleoalba*
Common dolphin	*Delphinus delphis*
Bottlenose dolphin	*Tursiops truncatus*
Risso's dolphin	*Grampus griseus*
Pilot whale	*Globicephala macrorhynchus*
Rough-toothed dolphin	*Steno bredanensis*
Melon-headed whale	*Peponocephala electra*
Fraser's dolphin	*Lagenodelphis hosei*
Pygmy killer whale	*Feresa attenuata*
False killer whale	*Pseudorca crassidens*
Killer whale	*Orcinus orca*
Dall's porpoise	*Phocoenoides dalli*
Whales	
Rorquals	
Blue	*Balaenoptera musculus*
Minke	*B. acutorostrata*
Sei	*B. borealis*
Bryde's	*B. edeni*
Ziphiids (beaked)	*Mesoplodon* spp.; *Ziphius cavirostris*
Sperm	*Physeter macrocephalus*
Dwarf/pygmy sperm	*Kogia* spp.

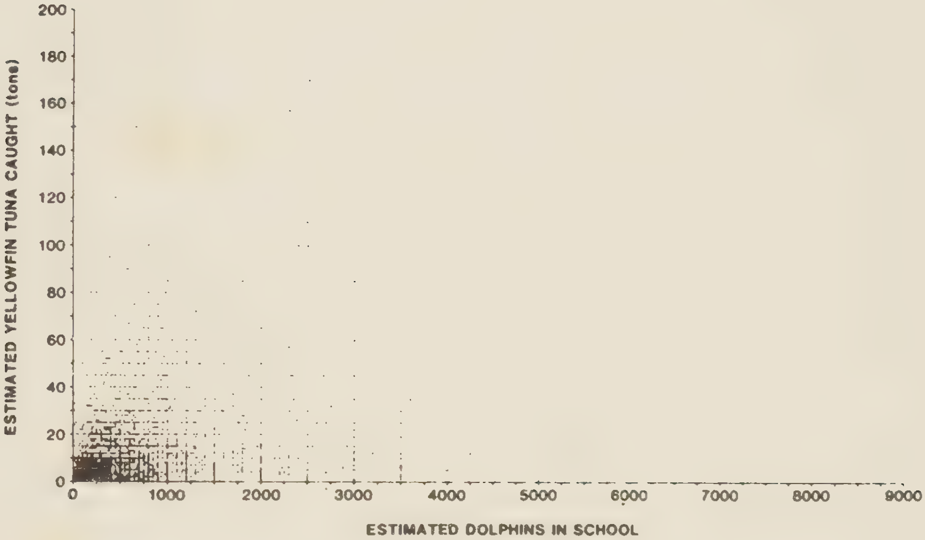
Appendix 5.2. Relationship between dolphin school size (numbers) and the catch (in short tons) of associated yellowfin tuna. Data collected by SWFC observers abroad U.S. purse seiners, 1981 through 1985.

	COAST–110°W LONGITUDE						110°W–140°W LONGITUDE					
	Porpoise fish[a]		*School fish*[b]		*All*		*Porpoise fish*[a]		*School fish*[b]		*All*	
YEAR	*n*	*(%)*	*n*	*(%)*	*n*	*(%)*	*n*	*(%)*	*n*	*(%)*	*n*	*(%)*
5°N–25°N Latitude												
1981	374	(97.6)	102	(79.4)	476	(93.7)	328	(95.7)	78	(24.4)	406	(82.0)
1982	378	(98.4)	67	(80.6)	445	(95.7)	179	(96.6)	74	(33.8)	253	(78.3)
1984	173	(95.4)	1	(–)	174	(95.4)	153	(94.8)	2	(–)	155	(93.5)
1985	728	(93.0)	24	(–)	752	(91.8)	157	(99.4)	0	(–)	157	(99.4)
1981–85	1,653	(95.5)	194	(76.8)	1,847	(93.6)	817	(96.4)	154	(28.6)	971	(85.7)
5°N–15°S Latitude												
1981	44	(75.0)	122	(33.6)	166	(44.6)	43	(81.4)	0	(–)	43	(81.4)
1982	166	(87.4)	55	(38.2)	221	(75.1)	68	(83.8)	4	(–)	72	(83.3)
1984	27	(92.6)	0	(–)	27	(92.6)	1	(–)	0	(–)	1	(–)
1985	11	(–)	0	(–)	11	(–)	0	(–)	0	(–)	0	(–)
1981–85	248	(86.3)	177	(35.0)	425	(64.8)	112	(83.0)	4	(–)	116	(82.8)

NOTES: These 1981–85 data are of sets (= purse seine launches) during a period straddling the 1982–83 El Niño event and during which time fishermen have often checked tuna schools for size before setting on the school. The data were collected by SWFC technicians aboard U.S. purse seiners. % = percentage of *n* tuna school set upon by the seiners that were with birds. (–) indicates unreliable percentage because of small sample size. There is no data for 1983.

[a] "Porpoise fish" = tuna schools associated with dolphins.

[b] "School fish" = not associated with dolphins.



Appendix 5.3. The percent of yellowfin tuna schools (n) (set upon by purse seiners) that were with birds, according to area and whether schools were with dolphins ("porpoise fish") or not ("school fish").